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AN EVALUATION OF THE FISHERY RESOURCES AVAILABLE TO CALIFORNIA FISHERMEN

by

ELBERT H. AHLSTROM

Introduction

My subject is the fishery resources available to California fishermen. Although I shall deal principally with large, underutilized resources, such as the anchovy, hake, jack mackerel, saury, and rockfish, I shall attempt also a cursory evaluation of the state of utilization of fishery resources in general off California.

Much of what I have to say here was first discussed in a paper entitled "Kinds and abundance of fishes in the California Current region based on egg and larval surveys," which I contributed to a symposium of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) on larval fish biology in 1963 (Ahlstrom, 1965). My laboratory has developed the method of using systematic surveys of fish eggs and larvae to evaluate the potential fish resources of the California Current region. It is possible to use fish eggs and especially fish larvae for resource evaluation because most marine fishes have a pelagic larval stage. The eggs and larvae of most pelagic fishes have a relatively shallow depth distribution, occurring principally in the upper mixed layer. This limited depth distribution simplifies the sampling problem.

The usual CalCOFI sampling pattern is shown in Figure 1. On CalCOFI surveys we haul our plankton nets obliquely from about 140 meters deep to the surface. This depth range completely encompasses the depth distribution of most of our common fish larvae, including the northern anchovy, Pacific sardine, jack mackerel, Pacific mackerel, and rockfishes (Ahlstrom, 1959). Eggs and larvae of Pacific hake occur principally below the thermocline; largest concentrations have been sampled between 75 and 100 meters deep. We may not completely encompass the depth distribution of hake eggs and larvae at all stations. On recent surveys we have again deepened our CalCOFI hauls—to approximately 210 meters—to ensure better depth coverage.

Our CalCOFI collections soon demonstrated that most of the larvae belonged to a relatively few kinds of fishes. By "kind" I am referring mostly to species, but sometimes to genus. In the earlier report I presented data on the relative abundance of the 25 most common kinds of larvae for the 4 years, 1955-58 (Table 1). In those years, the most numerous 12 kinds contributed over 90% of the larvae collected; the remaining 13 contributed about 5%. These data are fairly typical of all years, as only a few species have changed much in abundance over the 18-year span of the CalCOFI surveys (1949-66). The two most notable exceptions are sardine and anchovy. Abundance of anchovy larvae markedly increased during these years, while abundance of sardine larvae declined (Ahlstrom, 1967).

Based on CalCOFI egg and larva surveys, our major fishery resources, arranged in order of their relative abundance are: the northern anchovy, *Engraulis mordax;* the Pacific hake, *Merluccius productus;* rockfishes, *Sebastodes* spp.; and jack mackerel, *Trachurus symmetricus.* To these should be added the Pacific saury, *Cololabis saira.* I wish to discuss these five in some detail.

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Table 1—Comparison of Relative Abundance of Fish Larvae in the California Current Region Based on Yearly Summaries of Number of Larvae Obtained in Plankton Collection from CalCOFI Survey Cruises 1955-1958*

	1955			1956			1957			1958		
	No. Taken	% of Total	Rank[1]	No. Taken	% of Total	Rank[1]	No. Taken	% of Total	Rank[1]	No. Taken	% of Total	Rank[1]
Engraulis mordax	140,183	39.03	1	134,931	33.05	1	146,631	29.70	1	205,457	45.21	1
Merluccius productus	60,000	16.73	2	94,277	23.10	2	78,283	15.86	2	58,368	12.84	2
Sebastodes spp.	29,344	3.17	3	29,144	7.14	3	36,473	7.39	4	23,931	5.27	4
Citharichthys spp.	20,411	5.68	4	23,635	5.79	4	15,813	3.20	9	6,655	1.46	11
Leuroglossus stilbius	15,111	4.21	5	18,620	4.56	5	29,506	5.98	5	4,859	1.07	12
Sardinops caerulea	14,121	3.93	6	15,523	3.80	6	9,833	1.99	11	11,423	2.51	7
Trachurus symmetricus	13,246	3.69	7	8,027	1.97	10	20,006	4.05	6	6,409	1.41	10
Lampanyctus mexicanus	13,165	3.67	8	10,802	2.65	8	16,207	3.28	8	16,514	3.63	5
Vinciguerria lucetia	12,654	3.52	9	9,832	2.41	9	55,114	11.17	3	55,756	12.27	3
Lampanyctus leucopsarus	7,454	2.08	10	15,125	3.71	7	16,808	3.40	7	11,892	2.62	6
Diogenichthys laternatus	4,771	1.33	11	3,158	0.77	13	11,603	2.35	10	7,061	1.55	8
Bathylagus wesethi	3,245	0.90	12	2,146	0.52	17	6,347	1.29	12	7,021	1.54	9
Lampanyctus ritteri	1,988	0.55	13	1,924	0.47	18	2,789	0.56	14	3,091	0.68	13
Pneumatorphorus diego	1,950	0.54	14	1,520	0.37	20	1,865	0.38	18	1,273	0.28	20
Electrona spp.	1,823	0.51	15	1,852	0.45	19	1,415	0.29	22	1,775	0.39	15
Bathylagus ochotensis	1,301	0.36	18	2,231	0.55	15	1,078	0.22	25	1,550	0.34	16
Melamphaes spp.	775	0.22	25	1,051	0.26	24	1,328	0.27	24	1,255	0.28	21
Cyclothone spp.	1,532	0.43	16	814	0.20		2,880	0.58	13	2,795	0.62	14
Tarletonbeania crenularis	999	0.28	21	3,352	0.82	12	1,570	0.32	21	526	0.12	
Argentina sialis	832	0.23	24	1,288	0.32	22	1,400	0.28	23	276	0.06	
Prinotus spp.				2,470	0.60	14	2,731	0.55	15	1,307	0.29	19
Synodus spp.	641	0.18		958	0.23	25	2,338	0.47	17	1,219	0.27	23
Pleuronichtys spp.	1,038	0.29	19	1,118	0.27	23	579	0.12		164	0.04	
Diaphus theta	1,022	0.28	20	3,562	0.87	11	713	0.14		558	0.13	
Cynoscion spp.	860	0.24	23	104	0.02		31	0.06		1,350	0.30	18
Symphurus atricauda	73	0.02		1,373	0.34	21	1,603	0.32	20	222	0.05	
Ceratoscopelus townsendi	446	0.12		222	0.05		2,598	0.53	16	1,409	0.31	17
Symbolophorus californiense	653	0.18		462	0.11		1,645	0.33	19	1,236	0.27	27
Icichthys lockingtoni	1,385	0.39	17	898	0.22		768	0.16		438	0.10	
Palometa simillima	933	0.26	22	611	0.15		797	0.16		114	0.02	
Tetragonurus spp.	490	0.14		2,154	0.53	16	708	0.14		60	0.01	
Stomias atriventer	411	0.11		81	0.02		271	0.05		1,188	0.26	24
Hygophum spp.	400	0.11		223	0.05		795	0.16		993	0.22	25
All others	5,808	1.62		14,652	3.00		21,023	4.26		16,280	3.58	
TOTAL	359,155	100.00		408,140	100.00		493,549	100.01		454,455	100.00	

* Reproduced without change from Ahlstrom (1965).

[1] Rank includes only first 25.

Historically, research carried out by the Bureau of Commercial Fisheries (BCF) in California has centered on two kinds of fishes—sardines and tunas. The decrease in abundance of the Pacific sardine stimulated the cooperative research which became known as the California Cooperative Oceanic Fisheries Investigations (CalCOFI). The three main participants in CalCOFI were the California Department of Fish and Game, Scripps Institution of Oceanography (SIO), and the BCF. A major aspect of this research was the oceanic survey cruises, which sought to relate physical, chemical, and biological oceanographic features to the distribution, abundance, and survival of sardine eggs and larvae. The BCF was responsible for the egg and larva studies, which have provided information on most of our pelagic fishery resources in the California Current region off California and Baja California. To delimit the spawning distribution of the sardine, waters off Baja California have been investigated as thoroughly as those off California.

California has few natural harbors, and only a narrow continental shelf along most of its 1200-mile coast. These natural features have favored the concentration of the fishing industry in a few ports, and the exploitation of pelagic schooling fishes which could be caught in large quantities. These fishes have included the 4 tunas—yellowfin, skipjack, bluefin, and albacore—the Pacific sardine, the Pacific mackerel, the jack mackerel, and to a lesser extent the northern anchovy and squid. These species were used principally for canning. Reduction to fish meal and oil has been permitted for only two species—the Pacific sardine (1932-48) and the northern anchovy (1965 to date). The tropical tuna fishery is the most wide ranging of any carried out by U.S. fishermen. The tropical tunas are fished by California fishermen (in the eastern Pacific) from southern California to northern Chile. Fishes that yield a high return can profitably be fished in distant waters.

As background, I am including a tabulation of landings by California fishermen during recent years (Table 2). I have grouped the fishery resources into five cate-

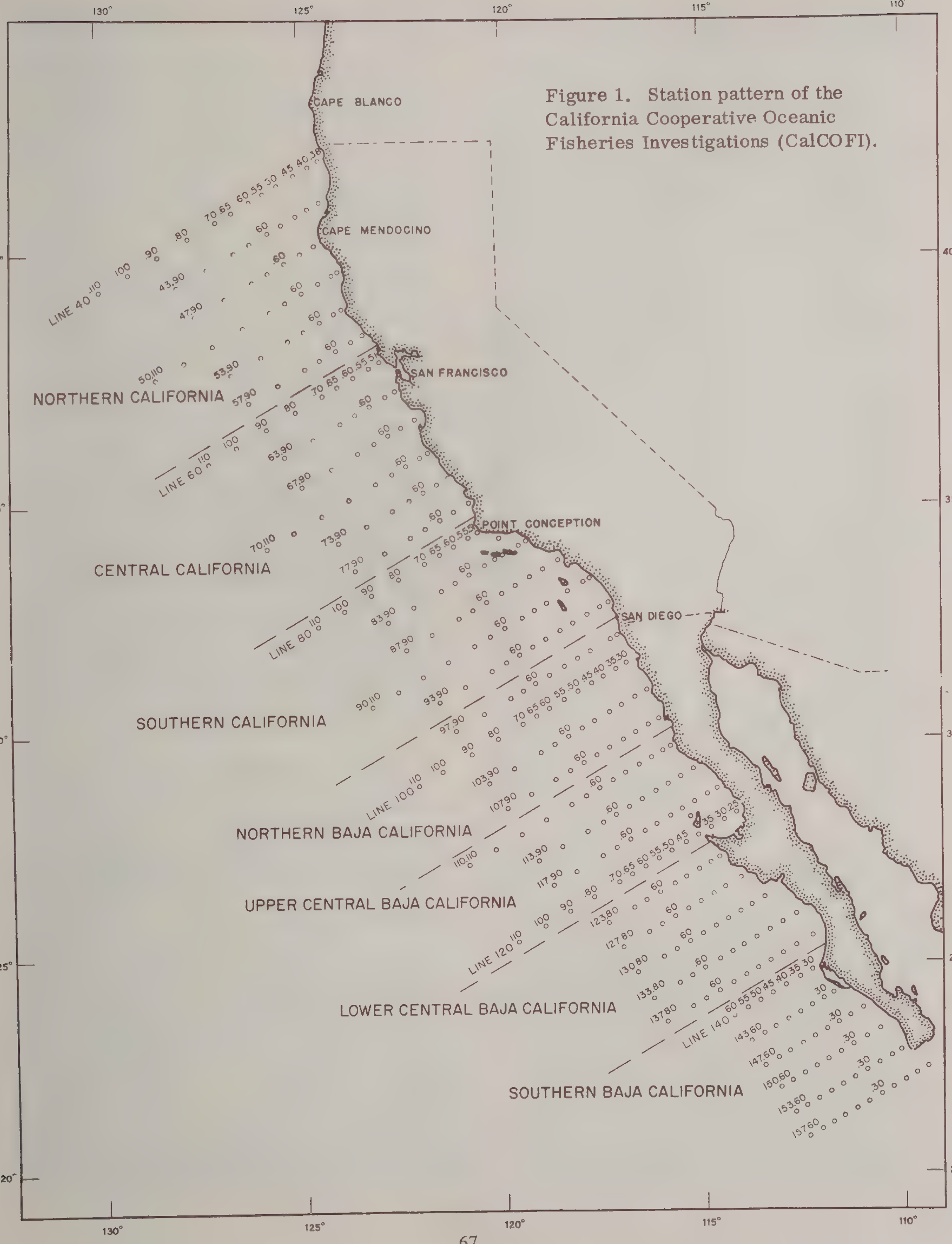

Figure 1. Station pattern of the California Cooperative Oceanic Fisheries Investigations (CalCOFI).

130°
125°
120°
115°
110°
40°
35°
30°
25°
20°
CAPE BLANCO
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
NORTHERN CALIFORNIA
CENTRAL CALIFORNIA
SOUTHERN CALIFORNIA
NORTHERN BAJA CALIFORNIA
UPPER CENTRAL BAJA CALIFORNIA
LOWER CENTRAL BAJA CALIFORNIA
SOUTHERN BAJA CALIFORNIA
LINE 40
LINE 60
LINE 80
LINE 100
LINE 120
LINE 140

Table 2. California fishery: Average yearly landings of fish and shellfish (in thousands of pounds) by California fishermen in 1955-60 and 1961-65, and landings in 1966

Fish and shellfish	Average yearly catch 1955-60	Average yearly catch 1961-65	Catch in 1966
Tuna and tuna-like fishes:			
Albacore	35,124	36,075	18,189
Bluefin tuna	18,182	24,307	34,820
Skipjack	95,651	81,009	51,089
Yellowfin tuna	141,467	146,206	132,595
Bonito	2,031	4,584	19,148
Yellowtail	306	175	245
Pelagic wetfishes:			
Anchovy	24,261	5,151	62,280
Jack mackerel	58,458	87,877	40,976
Pacific herring	1,770	840	242
Pacific mackerel	42,821	33,362	4,515
Pacific sardine	90,952	16,145	878
Squid	12,321	13,254	19,026
Bottom fishes:			
Flatfish	19,050	20,417	22,145
Hake	1,017	91	69
Lingcod	1,377	1,067	798
Rockfish	15,574	9,984	10,058
Sablefish	2,232	2,154	3,216
Misc. animal food	—	2,261	2,380
Other finfishes:			
Barracuda	947	506	319
White croaker	962	821	790
Salmon	6,712	8,478	9,445
White seabass	2,019	996	1,338
Shad	176	0	0
Sharks and skates	903	882	796
Smelts and whitebait	702	597	684
Swordfish	379	203	469
Other	1,685	1,429	1,662
Crustacea and mollusca:			
Crabs	16,698	4,938	12,674
Spiny lobster	575	489	487
Shrimps	1,817	1,687	1,228
Abalone	4,551	4,347	4,917
Clams (incl. mussels)	18	7	2
Octopus	14	30	18
Oysters	10,336	4,997	801
Total fish and shellfish:	611,088	515,366	458,299

* Corrected values.

gories: 1) tuna and tuna-like fishes, 2) wetfishes, 3) bottom fishes, 4) other finfishes, and 5) Crustacea and Mollusca. The catch for 1966 is listed separately and can be compared with average annual catches during the two immediately preceding 5-year periods, 1961-65 and 1956-60.

Tuna and wetfishes (including squid) made up 84-87% of the catch during these years. All are pelagic schooling fishes. These species were used almost exclusively for canning (except anchovy in 1966). The remainder of the catch, 13-16% of the total, was sold as market fish—fresh or frozen. About half of the market fish (and shellfish) were caught by bottom trawl gear and the remainder by a variety of gears (traps, crab pots, set-lines, hook and line, trolling, gillnets, round haul nets, diving, ...).

One noticeable feature of this tabulation is that the landings of most categories have either remained at a steady level or have decreased during recent years. The decrease in wetfish landings is particularly marked.

Table 3. Estimates of abundance of anchovy larvae, 1951-65

Year	Standard haul summations, based on monthly cruises (Ahlstrom 1966, Table 4)	Census estimates (in billions) (Ahlstrom 1967, Table 2)	Summation of average quarterly estimates (standard haul) (Ahlstrom 1966, Table 8)
1951	29,600	15,100	9,800
1952	59,600	17,100	20,600
1953	99,200	23,700	34,300
1954	161,200	38,400	56,700
1955	140,200	37,700	51,100
1956	134,900	38,500	51,400
1957	146,600	40,400	53,900
1958	205,700	56,900	75,100*
1959	206,800	54,200	72,700
1960	289,900	—	97,600
1961	—	—	97,100
1962	—	—	212,700
1963	—	—	200,500*
1964	—	—	161,900*
1965	—	—	261,200*

* Corrected values.

Had I taken an earlier period for comparison—1936-40, for example—the total catch would have been nearly 2½ times as large, and wetfish alone would have contributed 86% of the total. The wetfish catch in 1966 was barely 1/10 as large as the average yearly landings of wetfishes during 1936-40. Over this longer time span, the landings of tunas and market fishes would show about a twofold increase. Each of these had peaked, however, and had since remained static or decreased somewhat. I do not propose to discuss these landing statistics in any more detail than this.

ANCHOVY

Sources of Information

The body of information about the distribution and abundance of northern anchovy larvae parallels that for the larvae of the Pacific sardine. The first cooperative surveys of the BCF and SIO were made before World War II, in 1939-41, with the research vessel, *E. W. Scripps*. The 1939 cruise covered an extensive area between the Columbia River and Pt. San Eugenio off central Baja California. The 1940 and 1941 surveys (six survey cruises per year during the winter and spring) were concentrated in an area off southern California. Information on sardine egg abundance during 1940 and 1941 was given by Sette and Ahlstrom (1948). The basic data for collections of sardine eggs and larvae were presented by Ahlstrom (1948). Data on anchovy eggs and larvae for 1940 and 1941 were summarized by Marr and Ahlstrom (1948). The initial impetus for identifying anchovy larvae arose from their marked similarity in appearance to sardine larvae. Since they had to be carefully separated we reasoned that they should be enumerated and measured. If further justifications were needed—they were a potential fishery resource.

The egg and larva surveys were resumed on a modest scale in 1948, and on a vastly augmented scale in 1949 with the initiation of CalCOFI. Three research vessels participated in most CalCOFI cruises, which were spaced, with only a few gaps, at monthly intervals during 1949-60. They were made quarterly during 1961-65. In 1966, surveys again were made monthly. From these cruises we have amassed a body of information on the distribution and abundance of fish eggs and larvae that is without parallel in fishery investigations.

It is gratifying to be able to report that the sorting, identification, and enumeration of the eggs and larvae of sardines and anchovies from CalCOFI collections is almost current. The last cruise in 1966, made in December, is being worked up. With its completion, we shall have our body of data on these two species complete for the 18-year span of CalCOFI surveys. During the past 2 years, most of this information has been put on punch cards for computer processing.

Data on sardine and anchovy larvae for 1951-64 were summarized by Ahlstrom (1966). Through the cooperation of SIO, an atlas has been prepared which will illustrate the distribution and abundance of anchovy larvae on each CalCOFI cruise made during 1951-65. This atlas has the same format as others previously issued by SIO dealing with invertebrate and physical oceanographic features (Kramer and Ahlstrom, 1968).

Ahlstrom (1967) approached the problem of competition between sardine and anchovy larvae by examining the frequency of co-occurrences of the two species. As sardine larvae decreased in abundance, the frequency of their occurrence in hauls that also contained anchovy larvae markedly increased. In contrast, as anchovies increased in abundance, a much smaller portion of the positive hauls for anchovy larvae contained sardine larvae. Interestingly, both species occurred in larger numbers on the average when co-occurring, but survival rate was poorer. This trend is particularly noticeable in the anchovy data.

Distribution and Abundance Of Anchovy Larvae

I have summarized our estimate of abundance of anchovy larvae, 1951-65, in Table 3. Three different estimates are given for most years: 1) standard haul summations for 1951-60, the decade during which cruises were monthly, 2) census estimates for the same years (1960 estimate is not yet available), and 3) summation (standard haul) based on four quarterly cruises per year, or equivalent, 1951-65. Since these are the only estimates available for 1961-65, they are compared with quarterly values for the earlier years.

Standard haul summations.—Our counts of numbers of larvae taken in our "routine" oblique plankton hauls at CalCOFI stations are standardized to the number of larvae under 10 square meters of sea surface. The two essential pieces of information needed in deriving a standardization factor for a haul are: 1) information on the depth stratum sampled (determined from angle of stray of the towing cable) and 2) an estimate of the amount of water strained during a haul (based on revolutions registered on a TSK current meter fastened in center of mouth of the net). A standard haul total for a cruise is simply the summation of such values for all stations occupied; the yearly total for a species is a summation of monthly cruise totals.

Census estimates.—A census estimate is a somewhat more refined estimate of abundance than the standard haul summation. An areal weighting is applied to each station, to compensate for unequal spacing of stations. The technique was first described by Sette and Ahlstrom (1948).

Summation (standard haul) based on four quarterly cruises per year, or equivalent.—During 1961-65, CalCOFI cruises were spaced at 3-month intervals. Each cruise usually extended over 2 months, such as January-February, April-May, July-August, and October-November. Coverage of the CalCOFI pattern between San Francisco, California, and Pt. San Juanico, Baja California (station lines 60-140), was achieved on most quarterly cruises. Two station lines—line 60 off San Francisco, California, and line 90 off San Clemente, California—were extended seaward to station 200 (station 60.200 was approximately 600 miles off San Francisco and station 90.-200 was about 700 miles off San Clemente). For the years 1951-60, each quarterly estimate is the average of three or fewer comprehensive survey cruises.

Distribution.—In the California Current water off California and Baja California, most anchovy eggs and larvae are obtained between Pt. Conception, California, and Pt. San Juanico, Baja California. Larvae of the northern anchovy are seldom taken in any number to the south of Magdalena Bay, Baja California, and this species has not been taken in the Gulf of California. Abundance of anchovy eggs and larvae decreases off California as one goes north from Pt. Conception, and few have been taken off northern California. Abundance has been increasing off central California in recent years, however, especially in the area between Pt. Sur and Pt. San Luis (station lines 70-77). Anchovies are known to spawn off Oregon and Washington. These fish may constitute a separate resident population, distinct from anchovy stocks off California and Baja California.

During the majority of the 15 years summarized in Table 3, anchovy larvae occurred in greater abundance off Baja California than off California. Abundance was lowest off California during years with colder than average water temperatures during the winter and spring, such as 1956, and highest during years with above average water temperatures, such as 1957-59. For a more detailed discussion refer to Ahlstrom (1966).

Increase in abundance of anchovy larvae since 1951.—Abundance of anchovy larvae has increased spectacularly during the 15 years, 1951-65. On the basis of census estimates (our most sensitive measure of abundance) the increase in abundance between 1951-52 and 1958-59 was about 3-½ times. Between 1958-59 and 1962-65 the abundance of larvae again increased about 2-½ times. The anchovy population presumably has been expanding into the vacuum left by the decrease in the sardine population; it may have reached the optimal level of abundance consistent with its food supply.

Method of Deriving Present Estimate Of Abundance of Anchovy Population

Sometimes it is necessary to derive population estimates by use of an indirect method; the abundance of one species is tied to that of another. I will do this in deriving an estimate of abundance of the anchovy population. We have a good "fix" on the abundance of the adult sardine population in 1958. We also have good information on the abundance of sardine and anchovy larvae in that year, and in all years between 1951 and 1966.

The 1958 sardine season is used as a reference year because it was a year with a fairly substantial catch, especially as compared with adjacent years. The larger catch resulted from two circumstances: 1) the entry of a good year class (the 1956 class) into the fishery, and 2) high availability of fish to the California fishery resulting from the warm water prevailing during 1958.

The catch of sardines in the 1958 sardine season was:

California	103,971 tons
Baja California	22,334 tons
	126,305 tons

Because of the high availability of fish, fishing mortality during the season was high—up to 50%. At 50% fishing mortality, the size of the adult sardine population would have been about 250,000 tons. In placing a range of 200,000-250,000 tons on the size of the sardine population in 1958, I am being conservative.

I also have made a calculation of the size of the sardine population in 1958, based on our estimates of sardine egg abundance. The method of deriving such estimates of the number of eggs spawned was described by Sette and Ahlstrom (1948). The estimate of sardine egg abundance for 1958 is 89.6×10^{12} eggs (Ahlstrom, 1965, Table 3). MacGregor (1957) reported that the average number of eggs spawned per batch by female sardines was 263 ova per gram of fish weight. Sardine ovaries contain several size modes of yolked eggs, and the sardine has a prolonged spawning season. The number of batches spawned per female probably varies with age and with ocean conditions. Clark (1934) postulated that three batches would be matured, on the average; this value usually has been used in deriving population estimates from egg data.

The number of eggs that would be produced per ton of spawning females would be $(263 \times 3) \times (453.6 \times 2{,}000) = 717 \times 10^6$

263 = number of eggs per batch per gram weight of fish
3 = number of batches spawned
453.6 = number of grams per pound
2,000 = pounds per ton

The weight of the population of spawning females would be

$$89.6 \times 10^{12} / 717 \times 10^6 = 125{,}000 \text{ tons}$$

Assuming an equal weight of males, the sardine spawning population in 1958 had a weight of 250,000 tons.

I hardly need point out that this independent estimate of sardine abundance in 1958 is identical to that derived from the fishery.

As discussed previously, estimates of the abundance of anchovy larvae have been derived in several ways. Similar estimates are available for sardine larvae. I have determined the relative abundance of sardine larvae in relation to anchovy larvae, using two of these estimates for each species—one based on standard haul totals and the other on a census estimate.

Estimates of relative abundance of sardine and anchovy larvae in 1958

	Estimate based on summation of standard haul total (Ahlstrom, 1966, Tables 17 and 45)	Census estimate in billions of larvae (Ahlstrom, 1967, Tables 1 and 2)
Sardine larvae	11,430	2,830
Anchovy larvae	205,700	56,900
Ratio: sardine to anchovy	1:18	1:20

The anchovy is somewhat more fecund than the sardine. Information on fecundity of sardines was published by Clark (1934) and by MacGregor (1957). MacGregor has submitted a manuscript on the fecundity of the anchovy to *California Fish and Game*. He found that anchovies, on the average, spawn approximately two times as many eggs per unit weight of fish as do sardines.

MacGregor's determination is my basis for equating one sardine larva to two anchovy larvae. Comparison of estimates of egg abundance for the two species would be preferable to estimates of larvae. Such egg information is not available for the 1958 season (anchovy eggs were sampled quantitatively on the 1965 and 1966 cruises, but not in 1958). In equating two anchovy larvae to one sardine, I am assuming that we sample the larvae of both species equally well, and that the age span sampled (which is influenced both by rate of growth and rate of mortality) is comparable.

Based on proportion of 18 anchovy larvae to one sardine (the more conservative of the two estimates of relative abundance) and allowing for the greater fecundity per unit weight of the anchovy (2 to 1), the size of the anchovy population in 1958 would be.

1,800,000 to 2,250,000 tons.

The anchovy population has further increased in abundance, reaching a plateau that is about 2½ times as large as the 1958 population (Table 3). My estimate of the present size of the anchovy population is

4,500,000 to 5,625,000 tons.

Although the portion of the anchovy population (estimates based on counts of larvae) distributed off California is somewhat variable from year to year, it exceeded 50% in 1964 and 1966.

JACK MACKEREL

The jack mackerel resource is one of the most widely distributed in the temperate eastern Pacific, ranging from the Gulf of Alaska south to Cape San Lucas, and occurring at considerable distances offshore. Its distribution has been delimited only gradually, because it is more extensive than the area covered on our CalCOFI surveys, and the fishery covers only a fragment of the range. Jack mackerel are fished mostly off southern California. The southern California fleet catches jack mackerel along shore from Pt. Conception to San Diego and offshore around the Channel Islands and Tanner and Cortes Banks. In addition there is a small but variable fishery in Monterey Bay, and a moderate fishery out of Ensenada, Baja California.

Defining the Distribution and Abundance of Jack Mackerel

Survey of eggs and larvae.—The eggs and larvae of the jack mackerel were described by Ahlstrom and Ball (1954), who also discussed larvae distribution and abundance during 1950 and 1951. During these years jack mackerel larvae were taken in greatest abundance off southern California and adjacent Baja California between Pt. Conception, California, and San Quintin, Baja California. The center of abundance appeared to be between 80 and 240 miles offshore. Information on jack mackerel larvae obtained on CalCOFI cruises has been published through 1957. A paper is in progress which will bring the data on larvae up to date, i.e., through 1966.

On CalCOFI surveys, jack mackerel eggs and larvae usually are taken in largest numbers off southern California and northern Baja California. Their abundance decreases to the south of Pt. San Eugenio, off central Baja California, and they are seldom taken farther south than Magdalena Bay. The seaward extent of jack mackerel spawning usually is not delimited on CalCOFI surveys, although many station lines extend 250-300 miles seaward. This sampling defect was partly remedied on the quarterly CalCOFI cruises during 1961-65, by the occupation of two station lines with a seaward extent of 600-700 miles. On these lines jack mackerel larvae were taken as far seaward as 450 miles off central California and 550 miles off southern California. [Roedel and Fitch (1952) reported capturing large adults as far offshore as 600 miles west of Los Angeles Harbor.]

The most comprehensive simultaneous coverage of the North Pacific was obtained during Norpac, the multi-vessel survey of the North Pacific, conducted mostly during August 1955. On this survey, jack mackerel eggs and larvae were taken as far seaward as 150° W. longitude off Washington (1100 miles offshore). This was the seaward extent of the pattern occupied by the CalCOFI vessels participating in Norpac (Ahlstrom, 1956). Plankton samples collected on Norpac at 155-180° W. longitude and 40-50° N. latitude by the Honolulu laboratory of BCF contained no jack mackerel.

Farris enumerated jack mackerel eggs for 4 years, 1951-54 (Farris, 1958) and the survival rate of larvae for three, 1952-54 (Farris, 1961). For the first month of life of these larvae, he found a similar survival rate in all 3 years, of about one larva per 1000 eggs spawned. He found that jack mackerel eggs occurred mostly during a 6-month period, February through July. The month of peak abundance of eggs usually was May—of larvae, June. In three successive years, 1952-54, nearly 30% of each year's total of jack mackerel eggs were obtained on the May cruise. The mean temperature at which eggs were collected in all 4 years was 15.5° C.; about 60% of the annual spawning occurred within 1° C. of this value.

Surveys of adult jack mackerel.—Large jack mackerel had been captured as far offshore as 600 miles west of Los Angeles Harbor by Roedel and Fitch (1952). The northern limits of adult jack mackerel have been rather well defined by the high seas salmon sampling program of the International North Pacific Commission. Jack mackerel have been taken as far north as 57°30′ N. latitude in the Gulf of Alaska (Powell and Peterson, 1957) and as far west as 162° W. longitude (H. Larkin, personal communication). These records extend the published distributional range of 155° W. longitude (Neave and Hanavan, 1960). Jack mackerel were taken mostly during the summer in waters with temperatures above 11° C. (Neave and Hanavan, 1960). Although some surveys extended to 160° E. longitude, jack mackerel were not taken seaward of 162° W. longitude.

The jack mackerel fishery.—The jack mackerel fishery has been one of the major California fisheries since 1947, when the catch increased sharply from 7,547 tons in 1946 to 64,524 tons in 1947. The largest catch in a single year was 73,260 tons in 1952. The average annual catches during the first decade of the expanded fishery (1947-56) was 40,370; it dropped to an average annual catch of 34,850 tons during the second decade (1957-66). The catch in 1967 was barely half of the latter value.

The future of the jack mackerel fishery is hard to forecast. It is not a unique fishery, but rather an extension of the fisheries for sardine and Pacific mackerel. The rapid expansion of the jack mackerel catch in 1947, for example, was possible because vessels and gear already were available. All three species, jack mackerel, Pacific mackerel, and sardines, were harvested with round haul nets—purse seines or lampara. Even the mesh size in the net was compatible for the three species. (Smaller mesh is needed for fishing anchovies, for example.)

At present there is a moratorium on landings of sardines, and Pacific mackerel are exceedingly scarce. The anchovy reduction fishery has really not materialized. Even jack mackerel were hard to locate during 1967. The purse seine and lampara fleet that has harvested wetfish over the years is now greatly reduced in number and most vessels are old. The future appears bleak.

Abundance estimate—jack mackerel population.—Farris (1961) estimated the abundance of jack mackerel eggs in the CalCOFI area for 4 years, 1951-54. These estimates were based on procedures earlier developed for estimating sardine egg abundance by Sette and Ahlstrom (1948). Farris found that the abundances of jack mackerel eggs exceeded those calculated for sardine eggs by Ahlstrom (1954, 1959c) for the same years as follows:

Estimated abundance of sardine and jack mackerel eggs in the CalCOFI survey area during 1951-54 (in trillions)

Year	Estimated abundance of jack mackerel eggs X 10^{12} (Farris, 1961)	Estimated abundance of sardine eggs X 10^{12} (Ahlstrom, 1954, 1959c)
1951	873	611
1952	593	136
1953	736	440
1954	462	355
Average 1951-54	666	386

Within the area surveyed on CalCOFI cruises, the average abundance of sardine eggs during 1951-54 was only 57.5% of the average abundance of jack mackerel eggs.

The difference undoubtedly is considerably greater than the data show, inasmuch as the distributions of sardine

Table 4. Abundance of hake larvae (standard haul summations) in CalCOFI survey region off California and Baja California, 1951-60, 1966; summarized by areas

[Station lines given below each area]

Year	Northern and central California 40-77	Southern California 80-93	Northern Baja California 97-107	Upper central Baja California 110-120	Lower central Baja California 123-137	Southern Baja California 140-157	Total number of larvae
1951	857	13,132	42,817	2,315	3,497	196	62,814
1952	56	35,477	11,022	6,761	3,917	456	57,689
1953	20	7,349	15,457	3,761	3,800	8,866	39,253
1954	57	6,366	12,440	9,740	10,288	17,388	56,279
1955	0	4,978	15,991	23,553	2,843	12,725	60,090
1956	2	2,147	38,079	14,440	3,165	32,024	89,857
1957	17	31,968	26,247	15,156	3,020	1,875	78,283
1958	3,317	37,606	9,003	5,884	2,072	493	58,375
1959	4,115	11,858	273	414	956	41	17,657
1960	2,574	12,088	6,737	4,521	6,955	147	33,022
1966	18,211	41,286	8,241	770	3,827	—	72,335

eggs and larvae were effectively covered by CalCOFI cruises, but only a portion of the spawning range of the jack mackerel was included.

Our information on the fecundity of jack mackerel is about as limited as is possible—and still have any. We have such information for only one specimen, reported by MacGregor (1966), a female 215 mm in standard length (229 mm fork length) weighing 171 grams. According to information given in Fitch (1956), this female was probably 2 years old and was spawning for the first time. The fish contained two modes of eggs, one at 0.40-0.58 mm in diameter, the other at 0.18-0.39 mm in diameter. Each size mode contained an estimated 52,600 eggs. On the assumption that both modes would have matured and been spawned had the fish developed normally, this female would have produced 306 eggs/gram per batch or 616 eggs/gram during the spawning season.

It may be asked—how typical is this one determination? MacGregor made a comparison with the Pacific mackerel (six specimens examined) that averaged 304 ova/gram per batch. A much larger sample of Pacific sardines (40 specimens) gave a value of 263 ova/gram weight per batch (MacGregor, 1957). These values furnish indirect evidence that the per-batch figure is reasonable. Even if older fish were found to mature proportionate numbers of eggs per unit weight per batch, another problem remains: Will older fish mature the same number of batches per year as this young one, or more? I think that a top figure can be put on the number of batches that could be matured per year. As noted earlier, Farris obtained about 30% of each year's eggs during 1 month, usually May. If all females spawned during the peak month, and if earlier or later spawnings were all repeat spawnings by the same females, then the average number of batches spawned per female would not exceed 3-1/3 (I am assuming that it requires at least 30 days to mature each batch of eggs).

One can derive several estimates of abundance of jack mackerel, depending upon how many batches of eggs are assumed to be spawned on the average during a season. I am using two estimates:

1) Based on two batches per female (which corresponds to the specimen examined by MacGregor).
2) Based on 3-1/3 batches per female (which I assume to be a top figure, for reasons discussed).

The calculations were as follows:

Average number of eggs spawned per year, 1951-54: $666 \text{ X } 10^{12}$.

Number of eggs spawned per ton of spawning females per batch: $279.4 \text{ X } 10^{6}$.

Number of eggs spawned per ton of spawning females during 1 year:

a) If an average of two batches of eggs per female is assumed: $558.8 \text{ X } 10^{6}$.
b) If an average of 3-1/3 batches per female is assumed: $931.3 \text{ X } 10^{6}$.

Estimated number of tons of spawning females:

a) Two batches spawned per female: $666 \text{ X } 10^{12}/558.8 \text{ X } 10^{6} = 1.19 \text{ X } 10^{6}$.
b) Three and one-third batches spawned per female: $666 \text{ X } 10^{12}/931.3 \text{ X } 10^{6} = 0.71 \text{ X } 10^{6}$.

Assuming an equal weight of spawning males, the total population would weigh:

a) $(1.19 \text{ X } 10^{6}) \text{ X } 2 = 2.38 \text{ X } 10^{6}$ tons.
b) $(0.71 \text{ X } 10^{6}) \text{ X } 2 = 1.42 \text{ X } 10^{6}$ tons.

The adult spawning population in these years (1951-54) within the CalCOFI survey area was between 1.4 and 2.4 million tons. Jack mackerel egg data are not available for succeeding years. Abundance of jack mackerel larvae was as great in 1966, however, as during these years.

Year	Standard haul estimates of larvae
1951	18,853
1952	21,938
1953	7,941
1954	14,940
1966	18,990

Because the abundance of jack mackerel larvae was similar in 1966 and 1951-54, I think it is safe to use the above population estimates as representative of the present abundance of jack mackerel.

These estimates are minimal, inasmuch as they are based on spawning within the CalCOFI survey area. As noted

Table 5. Abundance of hake larvae (standard haul summations) in CalCOFI survey area off California and Baja California, 1951-60, 1966; summarized by months

Year	January	February	March	April	May-December	Total number of larvae
1951	222	6,751	41,548	13,411	882	62,814
1952	784	17,224	24,081	15,009	591	57,689
1953	9,206	19,116	8,045	1,544	1,342	39,253
1954	20,764	10,352	17,592	6,100	1,471	56,279
1955	13,356	28,973	12,535	4,757	469	60,090
1956	33,376	39,746	15,010	1,047	678	89,857
1957	1,278	37,998	34,589	4,047	371	78,283
1958	2,269	15,885	17,812	20,699	1,710	58,375
1959	1,215	10,902	1,570	3,494	476	17,657
1960	2,166	10,228	15,469	4,991	168	33,022
1966	28,823	29,617	—	13,464	431	72,335

earlier, our surveys do not encompass the complete spawning range of jack mackerel in the eastern North Pacific, although we have accumulated information that helps in delimiting this distribution. An educated guess as to the total jack mackerel adult population in the eastern North Pacific would place the figure at 1½ to 2 times that measured in the CalCOFI area. This estimate would give a population of adult jack mackerel of 2.1 to 4.8 million tons. This resource is large, indeed.

PACIFIC HAKE

The fact that the Pacific hake is abundant and widespread has been known since the early days of CalCOFI; in fact, within 2 months after the first cruise of the Cal COFI program in 1949, there was a newspaper account of the unusual abundance of hake larvae. The story implied that hake had just increased greatly in abundance. Such an evaluation obviously was premature. At that time we had no background of comparative estimates of abundance of this or of most other fishery resources. This background was to be supplied by our spawning surveys. What the news release should have emphasized was that our newly initiated surveys had immediately given us insights, almost revelations, into the abundance of a number of our fishery resources.

Studies on depth distribution of fish eggs and larvae showed that we were markedly undersampling hake eggs and larvae in 1949 and 1950. In 1951 our oblique CalCOFI hauls were deepened from approximately 70 meters to 140 meters. One immediate result was that our catch of hake larvae increased by an order of magnitude, from about 7,000 hake larvae in 1950 to 62,800 in 1951. Unlike most of our common pelagic fishes, whose eggs and larvae are distributed in the upper mixed layer, hake eggs and larvae occur mostly within or below the thermocline, and are most concentrated immediately below the thermocline.

Hake larvae ranked first in abundance in 1951, before the anchovy population began its spectacular increase. They were about equal in abundance to anchovy larvae in 1952, and since then have ranked second to anchovy in all years except 1959 and 1960. Abundance of hake larvae during 1951-60 and in 1966 is summarized by area in Table 4 and by month in Table 5. Quarterly cruises are inadequate for estimating yearly abundance of hake larvae; hence estimates for 1961-65 are omitted. The Pacific hake has the most limited spawning season of any of our abundant species within the CalCOFI area—spawning is limited to a 4-month period, January through April. In most years, 40-50% of the larvae were taken during the month of peak abundance. MacGregor (1966), who studied the fecundity of hake, was of the opinion that each female probably only matured one batch of eggs per season. This judgment was based, in part, on the shortness of the spawning season. Hake ovaries, however, were found to contain a range of sizes of yolked eggs, hence the fish potentially could have matured more than one batch per season. If all females were spawning during the month of peak abundance, and spawning in adjacent months occurred from repeat spawnings by the same females, each female could have matured only about two batches per season.

Hake eggs and larvae not only have an extensive north-south distribution, but can occur at considerable distances offshore. This fact was demonstrated most conclusively in those years when CalCOFI cruises were extended farthest offshore. In one such year, 1951, hake larvae were taken at the station farthest offshore on line 80 extending seaward from Pt. Conception (Ahlstrom and Counts, 1954). During the April cruise over 1,000 larvae were taken at that station (80.130) about 325 miles offshore. In 1953, another year with more than usual offshore coverage, hake larvae were taken as far offshore as station 90.130 which is over 400 miles off the southern California coast, but larvae were not collected at several stations occupied seaward of this. Hake larvae also were collected over 300 miles offshore from central Baja California.

Hake larvae have a variable areal distribution from season to season. In 1956, which was perhaps the coldest year of the CalCOFI series, over 97% of the hake larvae were taken off Baja California, and fully one-third of these were obtained off southern Baja California. In contrast, over 70% of the hake larvae were obtained off California in 1958, a warmer than average year, and an even larger percentage in 1959. Our low estimate of hake larvae in 1959 (the lowest estimate in the 11 years considered in Table 4) may have resulted from the majority of the population spawning to the north of the CalCOFI survey area. In most years the abundance of hake larvae fluctuated about a standard haul summation value of 60,000 larvae.

Although hake larvae are widely distributed over the CalCOFI survey area, they are sometimes clumped—one or more samples along a survey line may contain large

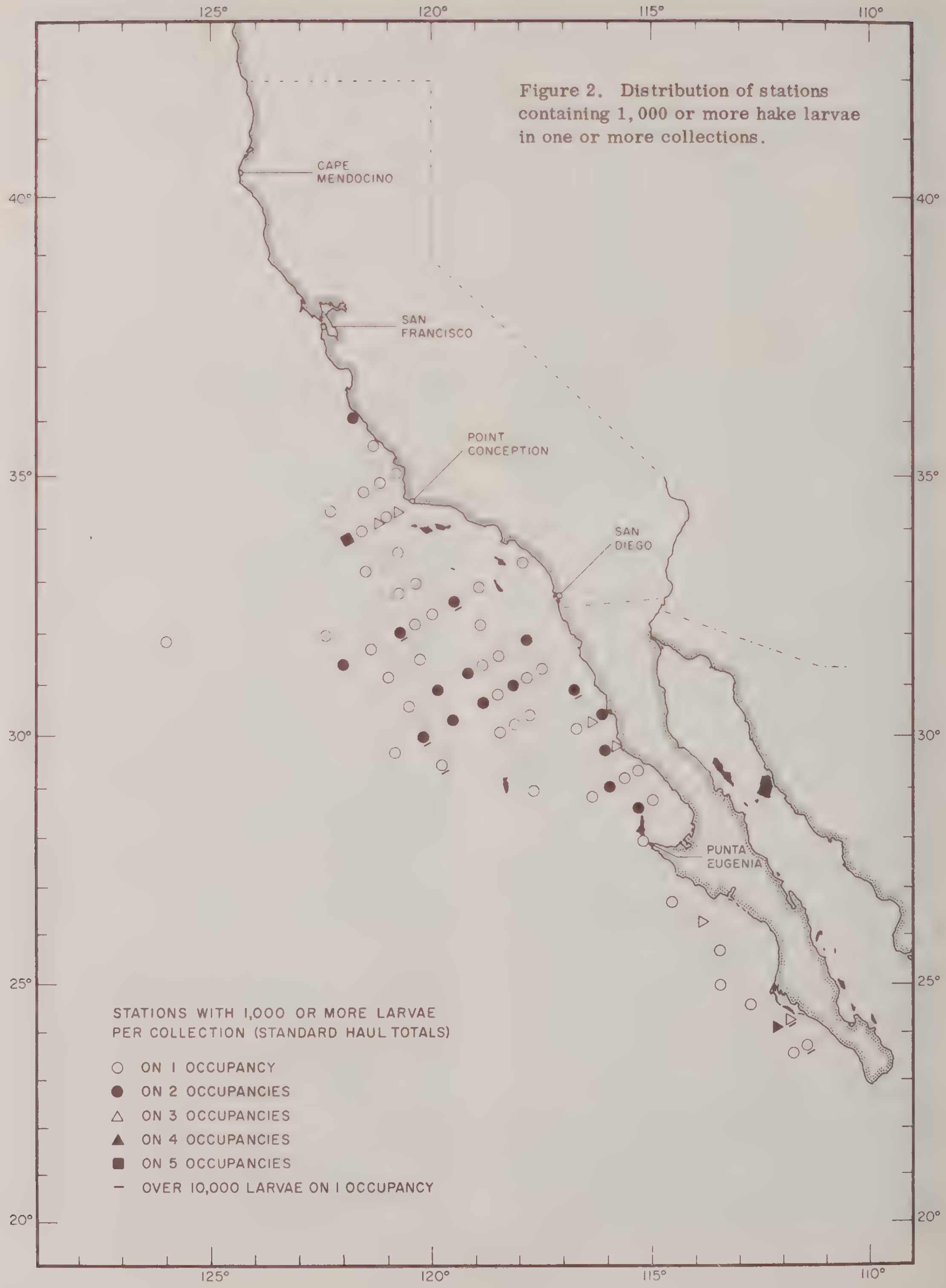

Figure 2. Distribution of stations containing 1,000 or more hake larvae in one or more collections.

125°
120°
115°
110°
40°
35°
30°
25°
20°
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
STATIONS WITH 1,000 OR MORE LARVAE PER COLLECTION (STANDARD HAUL TOTALS)
○ ON 1 OCCUPANCY
● ON 2 OCCUPANCIES
△ ON 3 OCCUPANCIES
▲ ON 4 OCCUPANCIES
■ ON 5 OCCUPANCIES
— OVER 10,000 LARVAE ON 1 OCCUPANCY

Table 6. Abundance (standard haul summation) by area of the larvae of rockfishes (Sebastodes spp.) in the CalCOFI survey region [Station lines given below each area]

Year	Northern and central California 40-77	Southern California 80-93	Northern Baja California 97-107	Upper central Baja California 110-120	Lower central Baja California 123-137	Southern Baja California 140-157	Total number of larvae
1951	4,086	7,946	3,214	2,426	960	35	18,667
1952	3,098	10,053	4,814	2,928	1,553	7	22,453
1953	1,848	20,112	6,110	4,759	3,201	15	36,045
1954	5,013	29,582	5,379	7,034	3,336	438	50,782
1955	2,893	14,571	3,721	6,336	1,796	24	29,341
1956	1,981	14,674	4,703	6,306	1,424	56	29,144
1957	3,170	23,163	3,779	4,878	1,466	17	36,473
1958	6,408	11,221	2,853	1,813	1,684	7	23,968
1959	3,230	5,231	916	1,399	696	20	11,492
1960	5,155	5,996	1,251	1,515	1,292	—	15,209
Percentage of yearly total							
1951	21.9	42.6	17.2	13.0	5.1	0.2	100.0
1952	13.8	44.8	21.4	13.0	6.9	<0.1	99.9
1953	5.1	55.8	17.0	13.2	8.9	<0.1	100.0
1954	9.9	58.2	10.6	13.8	6.6	0.9	100.0
1955	9.9	49.7	12.7	21.6	6.1	0.1	100.1
1956	6.8	50.4	16.1	21.6	4.9	0.2	100.0
1957	8.7	63.5	10.4	13.4	4.0	0.1	100.1
1958	26.7	46.8	11.9	7.6	7.0	<0.1	100.0
1959	28.1	45.5	8.0	12.2	6.1	0.2	100.1
1960	33.9	39.4	8.2	10.0	8.5	—	100.0

numbers of larvae. During 11 years, 1951-60 and 1966, 104 collections each contained 1,000 or more larvae (standard haul values). In such collections, recently hatched larvae usually predominated; hence the distribution of these hauls should reflect the distribution of spawning hake. Distribution of these collections within the CalCOFI survey pattern is shown in Figure 2.

In some areas hake larvae are taken in large numbers close to shore. Three such regions are: 1) Pt. Sur to Pt. Conception area off California, station lines 70-80, 2) the San Quintin area off northern Baja California, station lines 107-110, and 3) the vicinity of Magdalena Bay, station lines 143-147. The latter is an outstandingly rich area.

Off southern California and northern Baja California large concentrations of hake larvae have been obtained over a wide area, and some of the larger collections were as far offshore as 200-250 miles. In contrast, no large collections of hake larvae have been made from the Channel Island region off southern California.

If a fishery is developed on spawning hake, I assume that the fishermen first would concentrate in those areas in which the fish spawn rather close to shore.

Hake eggs and larvae have been sampled over a rather wide temperature range but most occur at 9-16° C. Rather detailed studies of the Pt. Arguello (California) area (which arbitrarily was given a 75-mile radius), showed that this area was marginal for hake eggs and larvae. Large numbers of larvae were encountered only during warmer than average years (1958 and 1959), and largest concentrations of larvae occurred at temperatures above 10.5° C. (10.5-12° C.). If hake usually spawn in waters warmer than 9° C. and spawning is heavy in waters warmer than 10.5° C., then conditions off northern California, Oregon, and Washington should be unfavorable for hake spawning during January-April in most years.

Estimate of Abundance of the Adult Hake Population

The main spawning of the hake population appears to lie within the CalCOFI survey area. We have not always delimited the offshore extent of hake eggs and larvae on our CalCOFI cruises. During warmer than usual seasons, such as 1959, a portion of the hake population may have spawned to the north of the CalCOFI survey area. Hence, our estimates of larval abundance are minimal.

Our information is limited to larvae. We have not routinely identified and enumerated hake eggs. Hence I cannot make the type of abundance estimate derived for jack mackerel.

If the problem were considered to be important enough, we could identify and enumerate hake eggs from previous surveys. We could also make a determination of rate of egg development as related to temperature, and use such information for determining the number of days of spawning represented in each collection. With these data, we could then make estimates of the number of hake eggs spawned during a year.

To convert such egg estimates to population estimates, we would need to know the average number of eggs spawned per batch per unit female weight (MacGregor, 1966, has determined this), the average number of batches that females spawn during a season, and the ratio of males to females (by weight) in the adult population.

The main statistics we do have are estimates of relative abundance of larvae. Hake larvae consistently have ranked second to anchovy. The abundance of hake larvae has not increased over time, as has that of anchovy larvae. In this respect the abundance of hake larvae is similar to that of jack mackerel larvae, which also have shown no consistent increase or decrease in abundance over time.

It has been noted that hake eggs and larvae are distriuted mostly below the thermocline, and hence develop at somewhat lower temperatures than do eggs and larvae of species that occur in the upper mixed layer. Ahlstrom and Counts (1954) pointed out that hake larvae were taken at temperatures between 9 and 16° C. (approximate mean 12.5° C.). Ahlstrom and Ball (1954) reported that 70% of the larger concentrations of jack mackerel larvae (50 or more per standard haul) occurred within a 2° C. temperature range, 14-16° C. (mean 15° C.). Hence hake larvae, on the average, develop at temperatures that are about 2.5° C. lower than for jack mackerel larvae. One consequence is that hake larvae, which develop more slowly, would thus remain longer in larval stages.

In fecundity and longevity hake are more comparable to jack mackerel than to anchovy. Hake larvae usually are three to four times as abundant as jack mackerel larvae. On the other hand, they develop at lower temperatures and hence probably remain for a longer time span in the larval stage. Also, we probably sample a larger portion of the total hake population on CalCOFI surveys than of the jack mackerel population.

The best informed guess I can make in the light of present information would place the minimal size of the hake population as equal to that of the jack mackerel and the maximal size as double that of the jack mackerel. Basing hake abundance on the most conservative estimate of jack mackerel abundance would result in an adult hake population of between 2 and 4 million tons. I consider these figures reasonable. The population I am considering is not confined to California waters, but rather is distributed from Cape San Lucas to British Columbia.

ROCKFISHES (Sebastodes Spp.)

Larvae of rockfishes (*Sebastodes* spp.) have ranked third or fourth in abundance in the CalCOFI survey area over the years. We use a generic designation, because presently we can identify the larvae of less than 1/2 of the species of rockfishes, and much of this ability has been obtained recently (Morris, 1956; Moser, 1967). Rockfishes can be identified to the generic level with certainty, however. The fishes of the family Scorpaenidae in California waters belong to three genera—*Sebastodes* with over 50 species, *Sebastolobus* with 2 species, and *Scorpaena* with 1 species. *Sebastodes* differ from the other genera in being ovoviviparous. Eggs are fertilized internally, and embryonic development occurs in the female. Larvae are extruded after hatching. In contrast, eggs of *Sebastolobus* and *Scorpaena* are spawned in gelatinous masses and fertilized after spawning.

Inasmuch as rockfishes occur only as larvae in plankton collections, we have to base our estimates solely on this stage. It is not possible to go back to our plankton collections and enumerate eggs, as could be done to improve our estimates of hake abundance, for example.

We do have information on fecundity of rockfishes (J. S. MacGregor, manuscript), and we do know that some species of *Sebastodes* mature more than one batch of eggs per year (Moser, 1967).

Rockfish larvae are often collected at considerable distances offshore. They have been taken over 320 miles off Pt. Conception, for example, and were taken in all years as far seaward as 150-250 miles on most major station lines. This widespread distribution of *Sebastodes* larvae parallels, at least in part, the widespread oceanic distribution of *Sebastes* larvae in the North Atlantic.

We have reported the abundance of rockfish larvae since the inauguration of our data series on fish eggs and larvae. Ahlstrom (1961) presented a paper on "Distribution and relative abundance of rockfish (*Sebastodes* spp.) larvae off California and Baja California" at the International Council for the Exploration of the Sea's Symposium on redfish. This paper dealt particularly with the distribution and abundance of rockfish larvae during 3 years, 1955-57 (the distribution of rockfish larvae in each of these years was illustrated).

Abundance (standard haul summations) of rockfish larvae in various subareas of the CalCOFI survey area are summarized by year for the years 1951-60 in Table 6. The average abundance during the decade was 28,700 larvae; all estimates are within half or double of this, except that for 1959. Rockfish larvae were most abundant off southern California—42.6 to 63.5% of the CalCOFI total were taken there. I am certain that our estimates off central California would have been much higher if our coverage of this area had been as consistent as our coverage of the area off southern California. Abundance of rockfish larvae decreases off Baja California, especially to the south of Pt. San Eugenio.

It would be pointless to attempt to make an estimate of the rockfish biomass, except in the most general terms. It is a very large resource, but it is a complex of many species—some of commercial importance, some not. Until we can sort out the pieces—until we can enumerate *Sebastodes* larvae by species—we cannot make a meaningful estimate of the potential of this resource. Certainly, the minimal potential is an order of magnitude greater than the present fishery.

PACIFIC SAURY

The other major fishery resource I wish to discuss, that of the Pacific saury, is not as adequately sampled by egg and larva surveys as the preceding fishes. Nevertheless, CalCOFI surveys have been our chief source of information about this resource. Information concerning the distribution and relative abundance of the saury in the Cal COFI region has been obtained from identifying and enumerating saury eggs in our plankton collections, and from visual observation of saury abundance while occupying stations in our CalCOFI pattern.

We do not know how quantitatively we sample saury eggs. They are unique among fish eggs sampled routinely in our plankton hauls in that they occur in clusters rather than singly. They have a feature, shared with many of their close relatives, the flying-fishes and halfbeaks, of having eggs attached to one another by fine filaments. The saury egg is ovoid—an unusual shape for planktonic eggs—and the filaments are grouped at one pole (except for one isolated filament that arises from about the middle of the long axis of the egg). It is also a fairly large egg that requires several times as long to hatch as eggs of the sardine or anchovy.

The saury egg is somewhat adhesive; we have observed them attached to plankton organisms, such as large salps. They also attach to floating objects, such as kelp. When we made a closely spaced grid study off central Baja California in 1951 (Kramer, 1963) using both a floating drogue and anchored buoy for station positioning, the attachment lines of each became clustered with saury eggs during their 5 days of immersion. A portion of the eggs remain free-floating and are collected in our plankton hauls. Occasionally, we sample a cluster of 100 or more eggs. Usually we sample small groups of eggs, 2 to 20 in a cluster, or pick up detached eggs.

Although saury eggs have been obtained in all months of the year on CalCOFI surveys, over 92% of the eggs have been collected during February-July and fully 65% during April, May, and June.

Saury eggs have been obtained only in about one haul out of 9; yet during the CalCOFI surveys they have been collected at every station occupied with any frequency except for a few inshore stations and some stations off southern Baja California. The saury, like the anchovy and jack mackerel, is a temperate-water species whose abundance decreases sharply off southern Baja California. It also is infrequently taken over shallow water. Within the CalCOFI region the distributions of saury eggs and larvae are remarkably similar to those of the jack mackerel. Both species decrease in abundance off southern Baja California, both tend to be more abundant offshore, and both have been taken as far offshore as our cruises normally extend. In fact, saury eggs have been collected at the outermost station on CalCOFI lines 60 (60.200) and 90 (90.200)—at distances 600 and 700 miles offshore, respectively. We found on Norpac that the saury had even greater offshore extent. Saury eggs were taken in the mid-Pacific (collections made by the BCF Honolulu Biological Laboratory) and jack mackerel eggs and larvae only out to 150° W. longitude. From this distribution we rightly concluded that the saury had an oceanwide distribution in the temperate north Pacific. The Russians have verified this point by experimentally fishing saury across the north Pacific along the northern limb of the oceanwide circulation pattern of the north Pacific. Among temperate-water species, the albacore, bluefin tuna, and saury have been shown to have an oceanwide distribution in the North Pacific. The two temperate tunas have been shown to migrate from one side of the ocean to the other (tag returns). It is probable that the saury would not move about this extensively—rather the population may be made up of several regional stocks.

Although data on saury eggs have furnished excellent information on the distribution of this resource, I do not consider the data particularly reliable for estimating abundance. We are not sampling the complete egg population. An unknown percentage of the eggs have become attached to floating objects, including animals, and been removed from the plankton community.

G. Orton found that saury eggs kept in a finger bowl at room temperature (ca. 18° C.) required 9 to 10 days to develop to hatching (personal communication). Although crude, this determination permits comparison of time required for embryonic development with species that have been more precisely studied, such as the anchovy (Lasker, 1964), or jack mackerel (Farris, 1961). As a rough estimate, embryonic development of the saury requires about four times as long as does this stage of anchovy development. Because of the prolonged embryonic period, the saury hatches at a more advanced stage of development than do most pelagic fishes. The newly hatched saury larva has pigmented eyes, a functional mouth, well-developed larval pectoral fins, and a functional caudal fin. It is an actively swimming organism at hatching. Its snake-like locomotion and its bursts of speed can be observed by watching small sauries that collect under our vessel's working lights at night. One consequence of this agility is that they dodge our plankton nets, and only the occasional specimen is caught. We could obtain much better information on the relative abundance of young sauries if we added a surface net haul towed at 5 to 6 knots to the set of observations we make at hydrographic-biological stations.

The saury appears to be distributed close to the surface. Its presence under working lights of our research vessels makes it the most conspicuous fish in the CalCOFI region. It could almost be called obtrusive. We decided to take advantage of this fact, and began a program of visual evaluation of saury abundance at all night stations. The data were summarized for the years 1950-55 in Ahlstrom and Casey (1956). Eberhardt (1954) discussed saury observations made during young fish surveys of the California Department of Fish and Game. Smith, Ahlstrom, and Casey at present are reanalyzing these data to incorporate in a paper dealing with this resource, which will be published in CalCOFI Reports.

The saury is one of the prime species sought by Japanese and Russian fishermen in the western north Pacific. The catch, after building to a level of over 1/2-million tons, has since declined. Soviet vessels have evaluated the potential of this ocean-wide resource off Oregon and California.

If an estimate of the adult saury population in the Cal COFI region were to be based solely on egg data, it would be a relatively modest-sized population of about 225,000 tons. The CalCOFI surveys cover only a portion of the saury's spawning range in the eastern Pacific. Even using this estimate, and assuming that half of the spawning occurs outside the CalCOFI area, we would set the adult population in the eastern North Pacific at about 450,000 tons. This is a minimal estimate. The actual size of the population may be several times this large. Certainly, visual evidence of abundance would suggest a larger population size, as would the known importance of the saury in the diet of predator fishes such as albacore (McHugh, 1952) and marlin (Hubbs and Wisner, 1953).

MESOPELAGIC FISHES

Among the abundant larvae in CalCOFI collections are those of mesopelagic fishes. These belong primarily to three families, the Myctophidae (lanternfishes), the Gonostomatidae, and the Bathylagidae (deep-sea smelts). In CalCOFI samples, these fishes usually contribute 20-30% of the numbers of larvae. Among the top 33 kinds of larvae collected during 1955-58, 20 were larvae of mesopelagic species (Ahlstrom, 1965). (It would not make any difference what years were selected from our CalCOFI surveys; the list of species would be almost identical.) Among the 20 kinds of deep-sea fishes, 10 were myctophids, 4 were deep-sea smelts, 2 were gonostomatids, and 4 belonged to other families. Berry and Perkins (1966) reported that 34% of fishes taken in pelagic trawl hauls were myctophiformes, mostly myctophids.

As one moves offshore, the proportion of larvae of mesopelagic species gradually increases over those of epipelagic species, and eventually they greatly dominate. I have examined the collections of fish eggs and larvae ob-

Table 7. State of utilization of principal fishery resources by California fishermen

[Arrows indicate current trend in degree of utilization]

Overutilized	Fully utilized	Moderately underutilized	Much underutilized
Pacific sardine	Yellowfin tuna	←Albacore	Northern anchovy
Pacific mackerel	Market crab	←Bluefin tuna	Hake
	Ocean shrimp	←English sole	Saury
	←Spiny lobster	←Petrale sole	Squid
	Abalone	Skipjack tuna	Mesopelagic fishes
	California halibut	Sand dabs	Sharks and skates
		Dover sole	
	Salmon	Rex sole	←Rockfishes
	White sea bass	Lingcod	←Sablefish
		Pacific herring	←Jack mackerel
		White croakers	←Bonito
		Smelts	

tained on the first multi-vessel EASTROPAC expedition, conducted during February-March 1967. An extensive area of the tropical eastern Pacific is being covered on EASTROPAC between 20° N. and 20° S. latitude and offshore to 130° W. longitude. Four research vessels participated on the first EASTROPAC cruise. The collections are typical of tropical oceanic waters generally. Almost 80% of the larvae belong to the three families noted above—Myctophidae, Gonostomatidae, and Bathylagidae. Of these families the least ubiquitous may be the Bathylagidae. This family made up only a minor percentage of larvae in the samples I examined from the International Indian Ocean Expedition when I visited the Indian Ocean Biological Centre at Ernakulam, India. The myctophids and gonostomatids were as dominant in the Indian Ocean collections as they are in EASTROPAC samples or in oceanic waters offshore from California. These are the dominant fishes (numerically) in oceanic waters around the world. They must represent a tremendous biomass. They may never be harvested commercially, however (I hope I am wrong).

Four factors mitigate against their value as commercial species.

1) Small size. The two most numerous fishes in the tropical eastern Pacific, based on larval abundance, are the gonostomatid lightfish, *Vinciguerria lucetia*, and the myctophid lanternfish, *Diogenichthys laternatus*. Adults of the former attain a length of 1½ to 2 inches; adults of the latter are seldom longer than 1¼ inches standard length.

2) Depth distribution. Although the larvae occur mostly in the upper mixed layer (above 100 meters deep), the adults live at much greater depths.

3) Mode of distribution. Adults of gonostomatid and myctophid fishes seldom occur in dense schools. *Benthosema* may be an exception.

4) Offshore distribution. The fish are most numerous in oceanic waters, at a distance from land.

When one considers the vast areas of ocean in which mesopelagic fish numerically dominate—perhaps in 80 to 90% of the total oceanic province, their total biomass must be huge. I will hazard the guess that the biomass of mesopelagic fishes—myctophids, gonostomatids, bathylagids, and associated families is at least as large as that of the resources that presently support our commercial fisheries.

STATE OF FISHERY RESOURCES OFF CALIFORNIA

(AND IN WATERS TO THE SOUTH)

In Table 7 I have given an estimate of the state of utilization of the principal fishery resources by California fishermen. I have derived the background information from a number of sources in addition to our surveys. In particular I wish to acknowledge the review articles on California Ocean Fisheries (to 1935, 1947, and 1960) assembled by the California Department of Fish and Game.

Overutilized Species

Two species have been overutilized—sardine and Pacific mackerel. There presently is a moratorium on sardine landings in California, although the fishery continues off Baja California. The decline of the sardine is due in part to overfishing, in part to environmental conditions that produced a succession of poor year classes, and in part to competition with a thriving anchovy population. Pacific mackerel landings have become inconsequential, but unrestricted fisheries continue for this species off California and Baja California. The fishery for Pacific mackerel gradually has been overexploiting this resource, since the peak year, 1935. The fact that the population was able to rebound at intervals, shows what resilience is possessed by exploited stocks. In recent years, however, a substantial fishery for this species also has developed at Ensenada, Baja California. Both fisheries are exploiting the same stock of Pacific mackerel; the resource has not been able to withstand this double drain.

Fully Utilized Species

Most fully utilized species are those that bring a high dollar return—tunas, shellfish, salmon, and some preferred market fishes. Yellowfin tuna in the eastern Pacific now has been under international regulation for several years. Quotas are set yearly on the take of ocean shrimp in California. Despite size limits, which are rigidly enforced, the catch of spiny lobster has been declining as fishing pressure increases. The abalone resource is approaching full utilization (size limits serve to protect this resource), as is that for the market crab (which exploits only larger males). The California halibut resource off California may be on the decline. This species brings a premium price to commercial fishermen, is prized by sportfisherman, and large specimens are particularly vulnerable to skin divers using spears. The California halibut resource is less fully exploited off Baja California. The salmon resource has held up remarkably well, considering that salmon is a premium fish, eagerly sought by both commercial and sportfishermen. The commercial fishery now is limited to ocean-caught fish. Other species that may be rather fully exploited include the white sea bass and perhaps the petrale sole, although I have placed the latter under moderately underexploited species.

Moderately Underexploited Species

Included in this group are species that can withstand a moderately increased catch, i.e., less than double the present catch, to species that probably can withstand sustained catches of three or four times the present level.

The two temperate tunas, albacore and bluefin tuna, have been shown to have a Pacific-wide distribution, and both are withstanding the combined fishing pressures of Japanese and U.S. fishermen. We may be able to increase the share of U.S. fishermen by furnishing them more precise information on where and when to look for fish (improving the forecast program already underway under the direction of Dr. Glenn Flittner of the BCF, La Jolla, California). The U.S. fishery for both species is on juveniles and young adults—the Japanese fishery, mainly on older fish. Dr. Flittner is of the opinion that the level of the sustainable yield of both species may soon be reached.

The tuna with the greatest potential for increased yield probably is the skipjack tuna. The large EASTROPAC program, with its multi-vessel survey cruises of the eastern tropical Pacific, is oriented toward obtaining background information that will help in understanding the distribution and abundance of this resource. Unlike the yellowfin tuna, the skipjack tuna does not spawn in any abundance in the region of the tropical tuna fishery in the eastern Pacific. The fishery is dependent upon juveniles and young adults which move in and out of the area of the fishery. The main body of the resource appears to be offshore.

Catches of a number of flatfishes could be increased—probably doubled—by fishing at deeper depths or by fishing off southern California—an area only recently opened again to trawl fishing. Among the species with potentially larger yields are the dover sole, rex sole, English sole, and sand dab. Several of the lesser prized flatfishes, such as the arrowtooth flounder, should be able to withstand considerably increased fishing pressures. Both the sablefish and lingcod should be able to support a fishery that is several times as large as at present. The sablefish is known to occur at depth in offshore areas, and may constitute a very large resource. Although the herring population of California is moderately small, it could withstand fishing pressures several times as great as at present. This also applies to the white croaker (kingfish) and the several smelts—osmerid and atherinid—harvested commercially. Except for the tunas and herring, all the above are market fishes.

Much Underutilized Fishes

If the yield of U.S. fishermen is to be markedly increased, it can only be accomplished by fishing the much underutilized species: northern anchovy, hake, saury, squid, rockfishes, and jack mackerel. These constitute the major fishery resources of California. I have spent most of my talk discussing these much underutilized species—particularly from the standpoint of their abundance. How to stimulate their use by the U.S. industry is the basic problem of the whole symposium. I have refrained from discussing the economic and institutional difficulties encountered in getting a small anchovy reduction fishery underway in California. I have not discussed the race that is developing between Russian and U.S fishermen to exploit the hake resource. The rapid expansion of foreign fisheries makes it almost certain that within a few years there may no longer be latent resources in any ocean; all may be under exploitation. The problem we are trying to answer is: Will U.S. fishermen and the U.S. public have their rightful share?

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WHAT MIGHT BE GAINED FROM AN OCEANWIDE SURVEY OF FISH EGGS AND LARVAE IN VARIOUS SEASONS

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WHAT MIGHT BE GAINED FROM AN OCEANWIDE SURVEY OF FISH EGGS AND LARVAE IN VARIOUS SEASONS

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This presentation is an extension of the talk I made 2 years ago, which was published in CalCOFI Reports, Vol. X. The first talk, presented at the Symposium on Larval Fish Biology was titled, "Kinds and abundance of fishes in the California Current region, based on egg and larval surveys."

We know a great deal about the kinds of fishes and their relative abundance in the California Current region off California and Baja California. Most of these fishes have a more widespread distribution than we cover on CalCOFI surveys. However, it is the exceptional species whose distribution is completely delimited by our surveys. *Bathylagus wesethi*, a deep sea smelt, is an example of a species that may occur wholly within our survey area. The eggs and larvae of the Pacific sardine and the Pacific mackerel have been effectively delimited in Pacific waters but both have sizeable populations in the Gulf of California that we have not surveyed regularly. The Gulf sardines are now known to be genetically distinct and resident only in the Gulf; hence they have not complicated our problems. In all probability this also will prove true for other fishes found in and out of the Gulf, e.g. Pacific mackerel, hake.

I would like to raise a basic consideration in conduct of egg and larva surveys. CalCOFI surveys initially were oriented to the studies of the Pacific sardine. This species was found to have a widespread and variable distribution, especially off southern California and along the length of Baja California. We had to survey a wide area of ocean frequently. From the standpoint of evaluating other pelagic fish resources from egg and larval surveys, this was a fortunate circumstance. Fortunately, we began the systematic identifications and enumerations of all our egg and larva material, at the inception of the CalCOFI cruises. We soon came to realize that we were investigating a complex of interacting species. Each had its own season of maximum abundance and distributional range. Furthermore, nothing was static. Temporal and areal distributions of each species changed in response to varying ocean conditions.

It is now my firm conviction that fish egg and larva surveys should never be oriented to a single species or genus. They should be ecologically, rather than species oriented. The whole complex of species should be evaluated. I have no sympathy or rapport with studies that specialize in a particular group of fishes, such as tuna, to the neglect of everything else. It costs so much money to conduct surveys at sea that, in comparison, the monies needed to fully work up the collections of fish eggs and larvae, once obtained, are quite modest sums.

I have gone through several changes of mind in thinking about my topic. At first, I was thinking principally of how informative Norpac had been. Norpac was the Joe Reid inspired, oceanwide survey of the North Pacific (from 20° N lat.) made principally in August 1955. If I were to place a subjective value on Norpac, I should say that it gave me insights that were worth many CalCOFI surveys. I am not derogating our systematic CalCOFI surveys. From these we have not only learned a great deal about our fishery resources, but also have documented changes in their abundance, such as the remarkable increase in the anchovy population. Although informative, limited surveys have to be placed in perspective. We are looking at a small fraction of the Pacific Ocean on our CalCOFI surveys and at partial distributions of most fishes. It takes wider-ranging surveys to delimit these.

But not exclusively oceanwide surveys. We could learn a great deal by increasing our coverage, both to the north and south of the CalCOFI area. I would like to illustrate this by discussing two species, the northern anchovy and the Pacific hake. As you see, I choose to lead gradually to the subject of oceanwide surveys.

Our CalCOFI surveys have pinpointed the importance of two pelagic fishes, the northern anchovy and Pacific hake. The larvae of these two species consistently have been the most abundant in the CalCOFI survey area. However, neither of the distributions of these species is completely delimited by our surveys.

Anchovy:

The distribution of the northern anchovy is "open-ended" at the northern end of our survey pattern. We have fenced it in very well at the southern end of its distribution and at its offshore extent. Unlike the sardine, it does not occur as far north as British Columbia. Furthermore, in 1949 and 1950 we sampled anchovy larvae in moderate abundance off Oregon. We have not been north of California since then on CalCOFI cruises, except on Norpac, so we do not know from larva surveys what the state of the anchovy population is off Oregon, Washington and British Columbia.

It is difficult to generalize from our survey data. For example, we know that abundance of anchovy larvae in plankton hauls decreases markedly as one goes from southern California to northern California. I would like to look for a moment at the data on numbers of anchovy larvae obtained from various parts of California. We usually divide the CalCOFI pattern off California into three areas that we simply term the northern, central and southern California areas. The northern California area extends from the Oregon border to just above San Francisco (station lines 40-57); the central California area extends from San Francisco to Point San Luis (station lines 60-77); the southern California area from Point Conception to the Mexican border (station lines 80-93).

Inasmuch as anchovy abundance has increased over the years, it is necessary to take such increase into account. For this example I am doing this simply by dividing the time span of surveys into two equal periods, the first is the 7 years of 1951–1957 and the second is the 7 years of 1958–1964.

The area off southern California has had the best coverage of any in the CalCOFI pattern. During the decade of the 50's, the area was covered on 9 to 12 cruises a year—average 10.7. The area off central California was covered on seven cruises per year, on the average. The northern California area has been surveyed only about 30 times since the inception of CalCOFI, and the last surveys made in this area were in 1960.

The number of anchovy larvae taken off southern California were 86 larvae per occupancy during the first 7 years, and 210 larvae per occupancy during the second 7 years. The number taken off central California was lower in both periods, but a marked increase in abundance has been evident on the station lines adjacent to the southern California area. Numbers of larvae taken on lines 70-77 averaged seven larvae per occupancy in the earlier period, but 100 larvae per occupancy during the latter period. The upper portion of this area, off San Francisco to Monterey, has been less productive—the increase being from less than one larvae per occupancy on the average to just over 10 larvae per occupancy.

Few larvae have been taken off northern California at any time. During the decade of the 1950's, anchovy larvae were taken in 17 of the 267 hauls made in the area; the average number per occupancy was only about 0.4 of a larva.

Since we have not surveyed this area since 1960, we do not know if numbers are now increasing there. Also it is dangerous to assume that because numbers are low off northern California they will also be correspondingly low off Oregon and Washington. Anchovy larvae could be markedly more abundant in the water off Oregon and Washington than off northern California. There is even the possibility that anchovies in the Pacific northwest constitute a separate genetic stock. We are looking into the latter possibility using blood antigens. The former can only be determined by systematic surveys for fish eggs and larvae off Oregon and Washington.

We are intensifying our surveys in the CalCOFI area during this coming year (1966) in order to have a base year of data about fish egg and larva abundance at the same time that a controlled anchovy fishery is begun. The surveys will not cover any area north of San Francisco. Obviously, to know the state of the anchovy population over its whole distribution we would have to survey the ocean off the Pacific northwest as intensively as we have between San Francisco, California and Magdalena Bay, Baja California. I would like very much to stimulate such coast-wide surveys.

The Pacific hake is of more immediate interest in the Pacific northwest. A fishery for that species is getting underway there. Hake are only seasonally present in the shelf waters off Washington. There is still speculation as to where they go during the off season. Do they move south to spawn in waters off California and Baja California? Or do they merely move offshore to spawn in waters off Washington and Oregon?

Since there is a large population of hake in shelf water of Washington in the summer and fall months, it should be an easy matter to determine if they move offshore to spawn. If they do, there should be plenty of eggs and larvae to sample. I would like very much to see this point resolved. My guess is that hake will not be found to spawn off Washington in most years, but that they may spawn there when the ocean is unusually warm.

This educated guess is based on several lines of evidence:

One of these is the distribution of hake eggs and larvae within the CalCOFI survey area. In most years, the greatest number of hake larvae are taken off Baja California rather than off California. The percentage of the CalCOFI total of hake larvae taken off Baja California has been as high as 97.6%. This was in 1956, a year colder than average. In contrast, 70% of hake larvae were obtained off California in 1958 and 90% in 1959, during warmer-than-average years. Hence, it appears that the distribution of hake spawning shifts markedly in response to ocean conditions.

Another line of evidence is the temperature range over which hake eggs and larvae are collected. Our data are from vertical distribution studies and from regular CalCOFI surveys. Hake larvae have been taken over a wide temperature range—8–16° C with most occurrences between 10.5–15° C.

As part of our study for the Atomic Energy Commission, we have looked at our larva from the Point Arguello area fairly intensively. Point Arguello is immediately north of Point Conception. We define the Point Arguello area as that within a 75-mile radius of the Point. Hake larvae were common in the Arguello areas only during years with warmer-than-average temperatures, especially 1958 and 1959. During these 2 years most temperatures, at depths where hake larvae occurred, were above 10° C.

I have spent some time looking at water temperature data from off Oregon and Washington at 75 and 100-meter depths—the depth range at which we take most hake larvae in the CalCOFI area. In a cold year, such as 1956, winter and spring temperatures at these depths ranged between 6 and 8° C. In 1958, water temperatures occasionally were above 10° C, but most observations were between 7° and 9° C. It seems to me that water temperatures in the Pacific northwest ordinarily are too low for hake spawning. To substantiate or disprove my conclusion, we need only systematic surveys for fish eggs and larvae off Oregon and Washington.

I have given my argument for more extensive egg and larva surveys in the eastern North Pacific which raises an interesting point. Such surveys are not particularly needed for hydrographic observations which have been made with fair frequency. The problem is simply that systematic collections of fish eggs and larvae were not an integral part of those surveys. There is an education problem here. We must sell fishery oceanographers on the value of egg and larva surveys for resource-evaluation.

Now to discuss ocean-wide surveys. I would like very much to see the equivalent of Norpac repeated in all seasons, but with more systematic coverage and with uniform methods of sampling fish eggs and larvae. Furthermore, to answer some of the questions I am going to pose, it would be necessary for one person to examine collections from all parts of the Pacific. The studies of fish eggs and larvae should be centralized, not particulated.

Broad-scale surveys are, of necessity, cooperative. Financing for such surveys does not come easy; surveys have to be justified. If we are to launch repeat Norpacs, I think that support will have to come from major fishery investigations, such as those dealing now with temperate tunas.

In this area, fortunately, some spadework has been done. The need for such surveys was recognized in one of the resolutions agreed upon at the FAO-sponsored "World Scientific Meeting on the Biology of Tunas and Related Species," held at La Jolla in July 1962. The resolution, numbered 10, is titled "Cooperative Study of Albacore and Bluefin Tuna in the North Pacific Ocean." One of the recommendations is for "further cooperative oceanographic surveys of the North Pacific Ocean such as the Norpac and EQUAPAC expeditions, for the purpose of obtaining synoptic coverage, preferably at all four seasons of the year."

We know little about spawning season and areal distribution of eggs and larvae of the two temperate tunas. In fact, there is some question as to whether we are able to identify the larval stages of the albacore. I am certain that this is a problem that would be resolved if we had adequate material.

The bluefin and albacore are two species of North Pacific fishes that travel across the Pacific. We know this from the capture off Japan of fish tagged off California and Baja California and vice versa. We do not doubt that both species must eventually be studied on an oceanwide basis. There are other species, common as eggs and larvae in CalCOFI collections, that we suspect must also have oceanwide distributions. Two species of particular interest are jack mackerel and Pacific saury. We have taken jack mackerel eggs and larvae 1,100 miles at sea off Washington in the Norpac collections. We have looked at fish eggs and larvae collected by the Bureau of Commercial Fisheries, Honolulu, on Norpac to see if we could extend the distribution of jack mackerel further seaward. Their samples were from the mid-Pacific. We found no jack mackerel eggs or larvae in these samples, but we did find saury eggs. Hence, present evidence supports the trans-Pacific distribution of saury, but it is inconclusive for jack mackerel. Additional systematic Norpac-like surveys, especially during the spring season, would permit better evaluation of jack mackerel distribution.

Having made my justification with bread and butter species (and, parenthetically, all of these offer very interesting problems), I will proceed to discuss taxonomic and distributional problems with some of the simon-pure species—those without any potential except their ecological role. There are many such as these, but I wish merely to select a few examples.

Among the abundant kinds of fish larvae we sample in the CalCOFI area are those of deep-sea smelts. The common deep-sea smelts belong to two families, Bathylagidae and Argentinidae. The larvae of both families are easier to identify to species than are the adults. This is one of the groups in which larval taxonomy is a distinct aid to adult taxonomy.

We had an excellent demonstration of this from material obtained on one of the first, wide-ranging cruises made by Scripps, "Northern Holiday," which worked into the Gulf of Alaska near the Aleutians. On looking over the fish eggs and larvae from the cruise, I was pleased to find eggs and larvae of a species of *Leuroglossus* quite distinct from those of the common *Leuroglossus* in the CalCOFI area. These eggs were half again as large as those of the CalCOFI. They went through a somewhat different embryonic development. The larva had more pigment than *Leuroglossus stilbius* larvae, but, most striking, they had 10 vertebrae more. They obviously belonged to a quite distinct species. These differences were not as apparent to ichthyologists working with adults. A Russian scientist first described the northern form as a subspecies of *Leuroglossus stilbius* under the name *schmidti*. An American ichthyologist proceeded to synonymize the two, finding no important differences. Neither of these scientists had looked at all trenchant characters, especially the number of vertebrae. When these characters were pointed out, the northern species was recognized as a valid one.

Interestingly, it is apparent that this northern species of *Leuroglossus* is the same fish that was described from skeletal material taken from fur seal stomachs by Lucas in 1899. He gave his skeletonized fish the name of *Therobromus callorhini*. Our northern species of *Leuroglossus* should be known as *Leuroglossus callorhini*. This first example is drawn from a problem that larva surveys helped resolve, but there are many more yet to be resolved.

Some of such problems are in the related family Argentinidae. From studies of larvae, we know we have four species of Argentinidae belonging to three genera in the eastern north Pacific. One of these which poses no problems is a species with a localized, neritic distribution, *Argentina sialis*. A second, *Mic-*

rostoma microstoma, is a widely distributed species, which occurs on both sides of the Pacific, in the Atlantic, and Mediterranean. The other two belong to the genus *Nansenia*; one has a subtropical to tropical distribution, the other a subarctic to temperate distribution. At least four species of *Nansenia* have been described from the North Pacific, two from the western Pacific, two from the eastern; one or more of these may be synonyms. Here again, larvae from both sides of the Pacific would help us resolve such problems. The larvae of *Nansenia* also are more distinctive than their adults.

Larvae are useful in helping to resolve taxonomic problems in other groups of pelagic fishes, for example, *Scopelosaurus*. This is an interesting deep-sea fish that is a curiosity as an adult. A few species have been described, from the Atlantic, South Pacific and off Japan. Adult material is limited to one or two specimens per species, these usually in poor condition. One species of *Scopelosaurus* is rather common in the CalCOFI area in larval form. It took us some time to figure out what kind of fish it was, since so little is known about adult *Scopelosaurus*. When we compared the larva material from the CalCOFI with larvae from Norpac, on Shellback, and off Peru and Chile on Step I, we found that there are some six species of *Scopelosaurus* in the eastern and central Pacific between California and Chile. This is another one of the groups of fishes that has very distinctive larval characters. The problem remains of what to call our CalCOFI species and most of the others. A species of *Scopelosaurus* was described by Mead and Taylor from a very young juvenile specimen taken off Japan. It could be the same species as occurs off California. This could be settled if larvae were available from all of the north Pacific Ocean.

Such examples could be multiplied, using larvae of myctophids, paralepedids, etc. There are a multitude of problems that could be clarified if adequate material were available for study from trans-Pacific surveys.

DISCUSSION

McGowan: If the objective of your proposed program is to study the total ecology of larval fishes, won't it be necessary to include in it organisms other than fish larvae? Usually the larval fish make up a very small proportion of the total number of individuals present in a plankton tow. This indicates that larval fish are living among an overwhelming number of invertebrates which are potential predators, prey and competitors.

J. Johnson: The Coast and Geodetic Survey will soon start an expanded program of routine surveys of physical properties of the oceans. Recently there has been considerable discussion on what biological sampling should be included in the C&GS ocean survey program. I should like to know what the consensus of the scientists in this group is as to how worthwhile plankton sampling would be on the ocean survey program. Should samples be collected even though there might be no immediate plan for their analysis?

(The answer seemed to be that it would be worthwhile to collect the samples.)

Stewart: For some time now, we have been deliberating whether to barge ahead and make such tows routinely or to wait for specific requests for specific types of observations in certain areas. When we have gotten such requests, we have filled them. The special daily tows for tuna larvae and copepods made from the PIONEER at the request of the Bureau of Commercial Fisheries' Honolulu Laboratory is an example. NASCO and others have reiterated the need for data for zoogeographical studies, but requests to BCF and to individual biologists to come up with a definition of exactly what they want to have, have not yet resulted in a biological survey component of the ocean survey being developed. When I approached BCF Honolulu in 1962, the answer I got was—'Don't take any more North Pacific plankton samples for us, we have more now than we can process'—so we did nothing on it. I maintain that the samples should be stored in the ocean rather than on a shelf somewhere if nobody is going to work them up.

Longhurst: Isn't the problem about whether or not to take a plankton sample rather one of curating than processing? Plankton samples taken when opportunity offers may not cost much to collect on top of the cost of an expedition and should cost little to curate if properly organized; yet a library of such samples can be of enormous use to future work.

McGowan: Since a zooplankton sample represents an ecological situation which exists at a particular place and time, no sample which has been properly collected should be thrown out; further, no opportunities to collect samples should be missed.

Blackburn: The sorting of planktonic fish stages can be kept reasonably current, provided that there are people with a lively interest in the information and that they are not snowed under with other jobs. If such work is important, it should be staffed in an adequate way—qualitatively as well as quantitively.

M. Johnson: With respect to (1) the accumulation of plankton samples which have not been adequately analyzed for their contents and (2) the reluctance to add to this burden by more plankton collecting because of lack of plankton sorting personnel and facilities, is it possible or practical to send samples to the Smithsonian Sorting Center in Washington, D.C., for sorting?

In light of the huge and growing plankton collection on this coast, I should like to propose that consideration be given to establishing a sorting center in this area.

Chapman: There is an International Sorting Center now in operation at Cochin-Ernakulum, Kerala State, India. It is working quite well. The United States has tens of millions of dollars' worth of rupees resulting from PL480 grain and other food shipments. They must be spent in India. The Sorting Center in Cochin requires additional support. Why can it not be given this from the PL480 rupee fund, plankton samples air-shipped from here to there for sorting under contract, and shipped back sorted with the only new cost to the United States being the air freight?

temperature on the growth of postlarval *P. aztecus* (Zein-Eldin & Aldrich, 1965). Animals held for one month at 11°C and 15-35‰ salinity showed excellent survival, but negligible growth, feeding, or other gross activity. Field observations by other workers indicated that young specimens of *P. aztecus* might be exposed regularly to winter and early spring temperatures in the coastal or near-coastal waters of the northwestern Gulf of Mexico (Baxter, 1963; Baxter & Renfro, 1966; St. Amant *et al.*, 1963). These observations suggested the need for a comparative study of the behavior of young shrimp at reduced temperatures. It seemed particularly pertinent to determine their ability to burrow when exposed to low temperatures, a response which might have survival significance in the natural environment as these decapods make the transition from a marine to an estuarine habitat.

MATERIALS AND METHODS

Postlarval specimens of *P. aztecus* and *P. setiferus* were collected from water about one meter deep near the beach at Galveston, Texas. Collecting gear consisted of a hand-drawn, 1-meter beam trawl suitable for retaining macroplankton (Baxter, 1963). All collections were made during July-August (of 1965), because at that season it is possible to find postlarvae of both species together in transit from offshore spawning grounds to estuarine nursery areas. Although most *P. aztecus* postlarvae appear at the bay entrance during March-April, we chose to test animals taken in July-August so that all shrimp came from comparable natural conditions. During collection, the water temperature ranged from 29 to 32°C, and salinity from 31 to 34‰. The animals were maintained in the laboratory at about 25°C and 25‰ for one to eight days before use in experiments. During this period, aeration was provided, and live larvae of brine shrimp (*Artemia salina*) were supplied as food.

For the behavioral studies, we used a small Plexiglass tank (240 mm long, 90 mm high, and 30 mm wide) containing approximately 50 ml of substrate collected from Galveston Bay and 300 ml of sea water. The substrate and water were about 10 and 60 mm deep, respectively. The water temperature was reduced by circulating cold water through 6-mm-diameter glass tubing which was partially immersed in the experimental tank (Fig. 1). Water for the cooling system was refrigerated and continuously recirculated by a cooler (A. Daigger & Co.). Rate of cooling in the tank was controlled by varying the amount of glass tubing that was immersed in the sea water. A 210-watt heating tape, placed under the tank and connected to a variable transformer, was used to control temperature differentials between water and substrate. Water and substrate temperatures were measured and recorded continuously with a Yellow Springs Instrument Tele-thermometer (Model 47) and recorder (Model

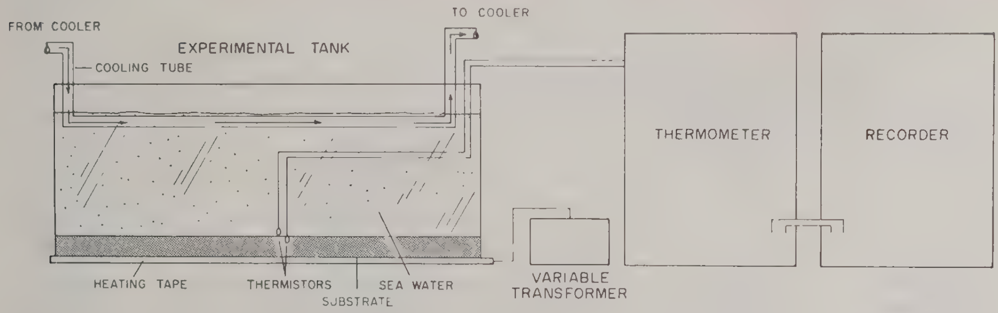

FIGURE 1. Experimental apparatus for the study of behavior of postlarval shrimp at reduced temperatures.

80). Thermistors attached to these instruments were located just above and below the water-substrate interface.

Preliminary observations suggested that rapid cooling rates and coarse texture of the substrate inhibited burrowing by postlarvae, whereas illumination stimulated such activity. Since one of our primary objectives was to determine and compare the burrowing abilities of *P. aztecus* and *P. setiferus,* we set up standardized test conditions which would neither stimulate nor interfere with postlarval burrowing. Cooling rates were reduced to 0.19°C per minute or less, and light was reduced to the level provided by two 40-watt, red, incandescent bulbs 150 mm behind the tank. A natural silty clay found to be suitable for burrowing was regularly used as the experimental substrate.

The substrate was collected from a natural bay shore by means of 25-ml pipettes with rubber bulbs attached to the pointed ends. A slurry of bay water and the upper layer (1-2 mm) of silty deposit was drawn into the pipette where the water was 50-75 mm deep. The material collected was 75 per cent clay, 22 per cent silt, and 3 per cent sand. (On one occasion, a *P. aztecus* postlarva which had burrowed into the substrate was taken in this process.)

One to 16 hours before each experiment, five specimens of *P. aztecus* and five of *P. setiferus* were introduced into the tank, and the light level was reduced to the experimental level. Shrimp behavior during this pre-experimental control period was taken as representing the type of activity exhibited by a given group of animals under experimental conditions in the absence of varying temperature. Burrowing did not occur during these periods. Throughout the experiments one of us monitored and controlled the temperature changes in the tank and recorded the observations of another person, who continually watched the shrimp. Our earlier runs were terminated when shrimp had either burrowed or lost equilibrium (lying on their dorsal or lateral surfaces). In later experiments, we also

TABLE 1
RESPONSES OF THE POSTLARVAE OF TWO SPECIES OF SHRIMP TO LABORATORY TEMPERATURE CHANGES

			Response to temperature decrease		Response to temperature increase	
Temperature regime	Species	Number tested	Number that burrowed	Per cent of total tested	Number that emerged	Per cent of total that burrowed
Decrease only	*Penaeus aztecus*	20	18	90	–	–
	P. setiferus	20	0	0	–	–
Decrease-increase	*P. aztecus*	30	29	97	29	100
	P. setiferus	30	0	0	–	–

made observations as the experimental tank and animals were returned to room temperature.

RESULTS

As experimental water temperatures were reduced from the initial (ambient) levels (24-27°C), several successive stages of shrimp behavior became apparent. The first stage, occurring in both species of shrimp at 16-21°C, was one of increased activity, during which the postlarvae swam about the tank continuously and rapidly. A further reduction of temperatures to 15-17°C caused an almost complete cessation of activity; the shrimp rested quietly on the substrate most of the time. A third and most marked stage of low-temperature behavior, usually taking place between 12 and 17°C, was regularly observed only in *P. aztecus* postlarvae. At that temperature range, these animals burrowed into the substrate. This was accomplished by means of abdominal undulations accompanied by movements of pereiopods and pleopods, as described for burrowing of adult penaeids by Dall (1958), Egusa & Yamamoto (1961), and Fuss (1964). In both species, further reduction of temperature to 10-12°C resulted in loss of equilibrium in those individuals which had not burrowed into the substrate.

Our most striking findings were (1) burrowing by postlarval specimens of *P. aztecus,* and (2) the inability of postlarval specimens of *P. setiferus* to burrow. Ninety-four per cent of the 50 *P. aztecus* postlarvae tested burrowed in response to reduced temperature, while none of 50 *P. setiferus* showed this type of activity (Table 1).

A size difference between these species of shrimp is characteristic for postlarvae collected along beaches in this area. The *P. aztecus* were 8.5-13

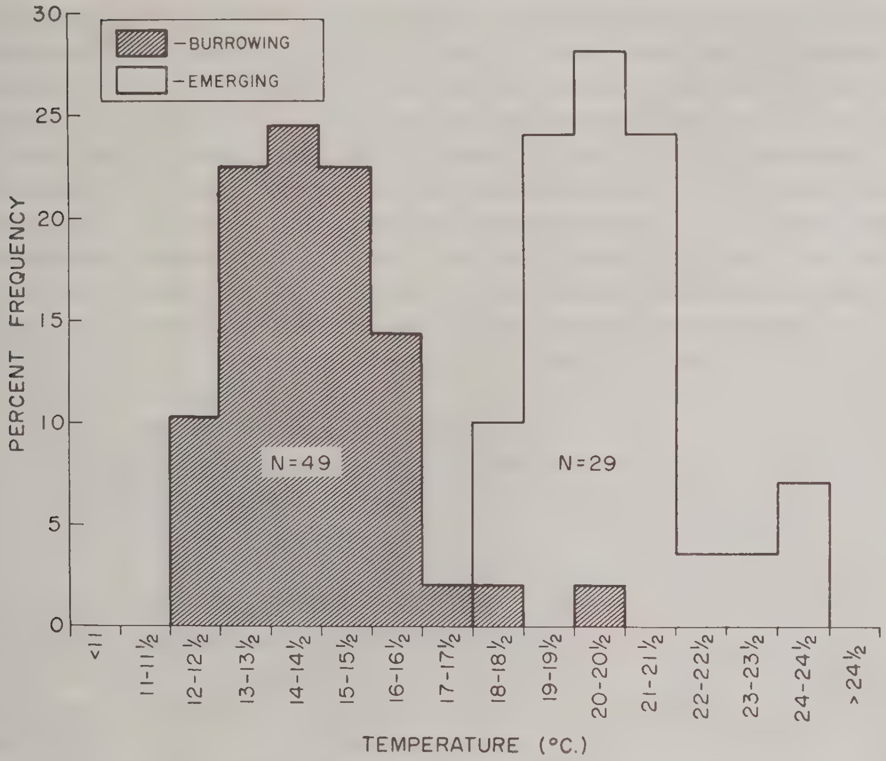

FIGURE 2. Per cent frequency distribution of burrowing and emerging of *P. aztecus* postlarvae at various temperatures. Shrimp which had not burrowed occasionally disturbed the buried animals, causing emergence followed by reburrowing in two instances. Hence, 49 instances of burrowing were observed among 47 shrimp.

mm in length, whereas the *P. setiferus* were only 6-8 mm long. The possibility that the postlarvae of *P. setiferus* were unable to burrow because of their smaller size led us to examine this possibility experimentally. Because larger postlarvae of this species were not readily obtainable alive from the field and are difficult to identify without injury, we used 10 specimens (11-17 mm in length) from a laboratory study of growth. Although the size advantage was now reversed in favor of *P. setiferus,* only one shrimp of this group burrowed when exposed to a temperature regime and substrate in which *P. aztecus* burrowed.

Several experiments were conducted to determine the effect of temperature differences between water and substrate on the incidence of postlarval burrowing. The tested differences (0.3°, 1.0°, and 1.2°C) had no significant influence on burrowing incidence of *P. aztecus.*

When sufficient experimental data had been collected to suggest that burrowing was a regular characteristic of the postlarval behavior of *P.*

aztecus, we conducted additional experiments, extending our observations to include an additional period during which experimental temperature was allowed to rise toward ambient levels (Table 1). This procedure provided data on the temperature range at which 29 postlarval specimens of *P. aztecus* burrowed and emerged. All of the animals which had burrowed emerged as the temperature reached 18-24.5°C. A frequency distribution of the temperatures at which postlarvae of this species burrowed and emerged shows that the two processes occur at markedly different temperature ranges (Fig. 2). Ninety-four per cent of the burrowing took place when temperatures were reduced to 12-16.5°C, while 86 per cent of the emerging occurred when temperatures rose to 18-21.5°C.

DISCUSSION

These results provide the first definite evidence of burrowing behavior in postlarval penaeid shrimp. The consistency with which reduced temperature elicited this type of activity in postlarval *P. aztecus* suggests that burrowing is a normal response of this animal to cold.

The absence of the burrowing response to low temperature in *P. setiferus* led us to compare the seasonal abundance and distribution of this species with that of *P. aztecus.* As reviewed by Williams (1965), in both *P. aztecus* and *P. setiferus* spawning and larval development occur at sea. The postlarvae then move to estuarine areas where they rapidly grow to subadult size (about 80-125 mm long) before migrating offshore to attain adulthood and spawn. There is a marked difference in the season at which postlarvae of the two species reach the bays. *P. setiferus* arrives at Galveston Bay during the summer, when water temperatures are consistently warm (about 25-32°C). Most individuals of *P. aztecus,* on the other hand, appear in March or April (Baxter, 1963), when bays are not only cool (averaging 15-25°C), but also subject to the drastic temperature reductions (often to 12°C) caused by atmospheric cold fronts (E. J. Pullen, in preparation). Thus, most postlarvae of *P. aztecus* are exposed to considerably lower and more changeable estuarine temperatures than those encountered by *P. setiferus.*

Although no definite evidence of postlarval burrowing has been reported from field investigations, the observations of St. Amant *et al.* (1963) are pertinent. In regard to *P. aztecus* postlarvae, they stated (p. 19): "The effect of cold water temperature or sudden drops in temperature is not altogether clear. Although the larvae may disappear completely from samples, we failed to note dead larvae in the sample after cold spells . . . ." (The temperature referred to was 11-12°C.) In view of our laboratory experiments, it now seems reasonable to suggest that burrowing, in response to reduced temperature, could have a significant effect on the availability of postlarvae to nets when water temperature is low, causing a temporary disappearance of these animals from samples. The ability to burrow in response to low temperature may have special survival significance for *P. aztecus* during this period of their natural history. Burrowing can serve both to attenuate rates of temperature change to which the animal is exposed and to protect it from predatory attack when temperatures are low enough to slow avoidance or escape movements (Fuss & Ogren, in press). On the other hand, a burrowing response to low temperature would have no obvious adaptive significance for *P. setiferus* because the seasonal characteristics of this species' life cycle are such that most postlarvae do not encounter cold temperatures in the northwestern Gulf of Mexico.

Burrowing may play a similar role of importance to *P. aztecus* postlarvae even before they move into estuarine nursery areas. D. L. Harrington found temperatures of 11°C at 4 fathoms to 17°C at 25 fathoms off Galveston in January and February, 1963 (in preparation). Levels for June through September ranged from 20 to 31°C. His data for 1964 indicate a similar pattern. It is clear that winter offshore temperatures are commonly within or below the range which we have experimentally shown to stimulate burrowing by *P. aztecus* postlarvae.

In this connection, it is interesting to consider the relationship between natural water temperatures and the arrival of these organisms in bays. In regard to *P. aztecus,* St. Amant *et al.* (1963) stated: "Maximal postlarval densities apparently do not appear in Louisiana until water temperatures remain above 20°C" (p. 18). A similar course of events can be determined for Galveston Bay, Texas, from the field data of Baxter & Renfro (1966). They took simultaneous water temperatures and macroplankton samples semiweekly for 4 years at the entrance to Galveston Bay. A total of 376 samples yielded 32,093 *P. aztecus* postlarvae. More than half of the shrimp (58.1 per cent) were taken at temperatures of 18-22°C, a range which included only 17.5 per cent of the 376 temperatures recorded (Fig. 3). This nonrandom distribution suggests a marked relation between temperature and the occurrence of postlarvae. The pattern is quite similar to that shown above for temperature and the emergence of burrowed shrimp from the substrate.

Two additional points relating to collections of *P. aztecus* postlarvae made at temperatures outside the "laboratory emergence" range (Fig. 3) strengthen this comparison of laboratory and field data. First, the only sizable collection of shrimp made at a water temperature below 19°C yielded 1,682 specimens, taken at 16°C on April 4, 1962. It is noteworthy that this temperature represented an unusually low departure from the existing general trend. Temperatures for the two weeks preceding this collection ranged from 19 to 24°C, and those for the following two-week period were between 20 and 25°C. Secondly, most postlarvae collected at

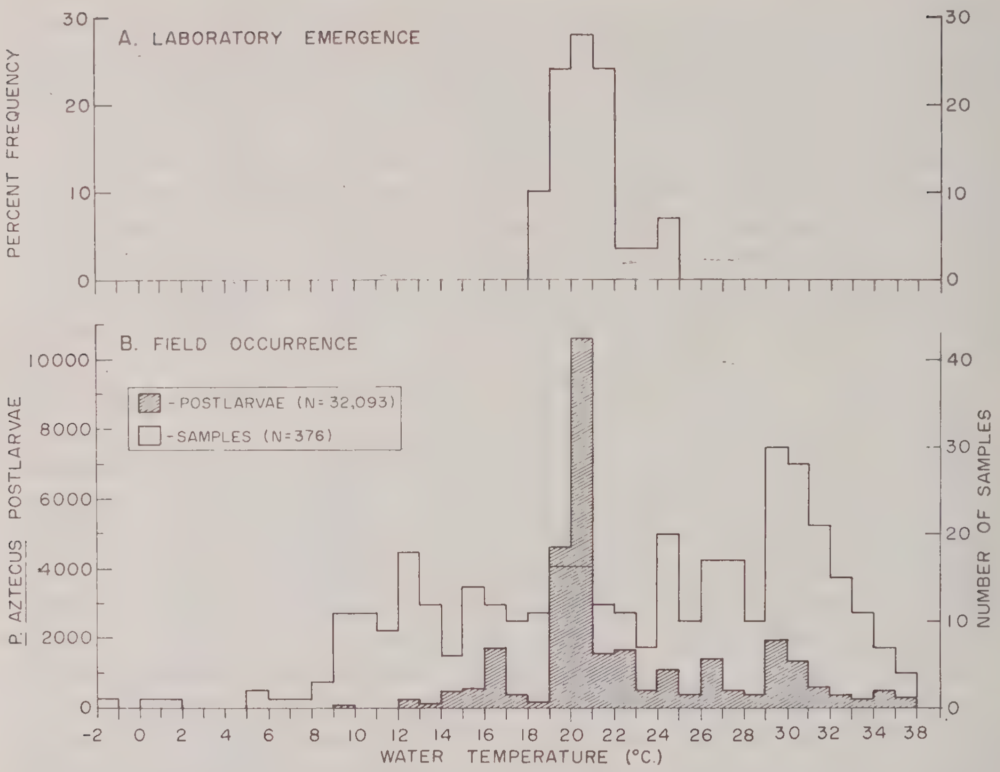

FIGURE 3. Temperatures associated with emergence of postlarvae of *P. aztecus*: A, Per cent frequency of postlarval emergence from substrate at various temperatures (laboratory results from Fig. 2); B, Frequency distribution of postlarvae collected at different temperatures at the entrance of Galveston Bay, 1960-63 (data from Baxter & Renfro, 1966).

temperatures of 25°C and above were taken during the summer and early fall. Cook & Murphy (1966) have shown that, after being spawned in the laboratory, young specimens of *P. aztecus* require from 2 to 3 weeks to reach the postlarval stage of development at 24 to 30°C. Thus, postlarvae arriving at bays in the summer and fall could never have been exposed to temperatures capable of inducing burrowing. For this reason, summer and fall collections could logically be excluded from field data to be examined for evidence relating to the hypothesis that postlarval *P. aztecus* burrow in response to winter temperatures. In any case, the agreement between laboratory and field results is sufficient to support this hypothesis. Thus it is possible that postlarvae of *P. aztecus* burrow into the substrate for part of the winter before entering the bays in early spring.

Further support for this interpretation may be derived by considering seasonal changes in the size of *P. aztecus* postlarvae in relation to the influence of temperature on growth. Baxter & Renfro (1966) showed that specimens of *P. aztecus* were larger in the spring than those collected at other seasons. The modal lengths were 12-13 mm for shrimp arriving at the bay during March-April, but only 10 mm for those taken in June through September. Zein-Eldin & Aldrich (1965) and Zein-Eldin & Griffith (1966) found that temperatures of 11-15°C greatly reduced postlarval growth, but permitted survival. Growth was only 0.0-0.6 mm per month at 11-15°C as compared with 9-23 mm per month at 20-30°C. Recalling Harrington's offshore water temperature data (given above), we infer that the growth rate of postlarval shrimp is less in winter than in summer and fall. This line of reasoning leads us to interpret the large size of *P. aztecus* postlarvae in the spring as the possible result of an extended period of slow growth offshore. If these animals were spawned in January or February, they should be smaller, not larger, than the fast-growing, summer-fall group on arriving at bays in the spring. On the basis of available evidence it seems reasonable to suggest that *P. aztecus* postlarvae reaching the bays in spring were spawned late in the preceding year.

The presence of *P. aztecus* postlarvae in the substrate offshore during December-February remains to be demonstrated. Final proof of postlarval hibernation in this species, and the importance of the burrowing mechanism to such a process, will await such evidence. The present work, however, characterizes *P. aztecus* postlarvae as having a rather specialized behavioral mechanism which seems well suited to protect this organism during the periods of torpidity induced by low temperature. Furthermore, the temperature range shown to elicit the burrowing response in the laboratory is commonly found during winter along the Texas-Louisiana coasts, where this species flourishes. Likewise, emergence of postlarvae in the laboratory was induced by a temperature range remarkably similar to that observed in nature when *P. aztecus* postlarvae enter bays during March or April.

Thus, laboratory evidence suggests that seasonal patterns of temperature distribution are adequate to induce burrowing by *P. aztecus* postlarvae during the winter and emergence in early spring, a sequence of events that fits in well with existing information regarding the seasonal occurrence of postlarval specimens of *P. aztecus*. We conclude that burrowing is a normal part of postlarval behavior in this species and represents an ecological mechanism through which it survives cold periods until temperatures more favorable for activity, feeding, and growth prevail.

ACKNOWLEDGMENTS

We acknowledge the cooperation of our colleagues at the Biological Laboratory, Galveston, Texas: M. J. Lindner, R. F. Temple, R. J. Berry, H. L. Cook, D. L. Harrington, and E. J. Pullen. Our discussions with them of their most recent findings have allowed us to explore realistically the potential significance of our experimental results. We are indebted to C. R. Mock for analyses of substrates.

SUMARIO

UNA INTERPRETACION ECOLOGICA DE LAS RESPUESTAS A LAS BAJAS TEMPERATURAS EN LAS POSTLARVAS DE *Penaeus aztecus* Y *P. setiferus*

Se presenta la primera evidencia reportada sobre la habilidad de las postlarvas de los camarones peneidos de enterrarse en un substrato.

Las postlarvas de *P. aztecus* se enterraron respondiendo a una reducción experimental de las temperaturas (usualmente dentro de una variación de 12°-17°C) y emergieron de 18°-21.5°C.

En los mismos experimentos, postlarvas de *P. setiferus* no se enterraron en respuesta a temperaturas bajas.

Se discute esta diferencia de conducta entre las especies en relación a sus respectivos patrones estacionales de abundancia de postlarvas. Se sugiere que el enterrarse es un mecanismo por medio del cual las postlarvas de *P. aztecus* sobreviven lejos de la costa por lo menos durante una parte del invierno y en las áreas estuarinas al principio de la primavera.

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issues and programs . . .

Bureau of Commercial Fisheries

DEPARTMENT OF THE INTERIOR

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The role of government, both federal and state, in relation to our fisheries has been subject to widely varying opinion. Perhaps most simply stated, the primary task of government is to develop basic knowledge about the fishery resources and their environments. This knowledge will then provide guidelines for managing existing fisheries so that they produce at a high level, and provide background information on under-utilized and non-utilized fishery resources for the fishery industry to use in determining what to fish, where to fish, and how to fish. For both categories, there must be included basic facts relating to size and nature of the resources, most economical harvesting methods, development of new processes and products, and an assessment of potential market. These activities are designed to strengthen the industry and conserve the resources. Some fishing industry problems are country wide but more are regional. Our discussion today follows in the latter classification.

REGIONAL ISSUES FOR FISHERY RESOURCES

As related to the Bureau of Commercial Fisheries objectives, there are two principal issues in the Gulf of Mexico.

1) Develop the vast potential of the under-utilized and non-utilized commercial fishery resources and

2) Acquire, for those fishery resources now the subject of established fisheries, the knowledge necessary to develop and maintain them at the highest possible level of productivity.

Of the under-utilized and non-utilized fishery resources, several species are prime targets for future attention.

Thread Herring and other Surface Schooling Species

Scientists at our Exploratory Fishing and Gear Research Base at Pascagoula, Mississippi, have estimated a two billion pound standing crop of thread herring in the Gulf of Mexico. In addition, there are large quantities of Spanish sardines, scaled sardines, and various anchovies.

A small fishery for thread herring has been established on the west coast of Florida but is experiencing difficulties in harvesting techniques. Our Pascagoula base is working to develop a sonar survey technology to determine school size. This involves simultaneous aerial photography and sonar observations on schools of fish in conjunction with commercial operations to determine exact size of the schools.

Purse seines now being used have limited capabilities in catching these species, especially in deep water. The Bureau's Gear Research unit at Pascagoula is working with industry to develop more efficient methods in harvesting of thread herring and related species.

A program to study the biology of thread herring and other surface schooling species has been recently initiated at our Biological Laboratory at St. Petersburg Beach, Florida. Field work now underway will provide information on life histories, growth, migrations, and distribution. These data will form the basis for subsequent studies having direct application to the commercial fisheries—tagging, population dynamics, mortality, and forecasting. The staff will work in close cooperation with the Pascagoula units.

Yellow-eyed Snapper and Tile Fish

The staff of our Pascagoula Base believes that yellow-eyed snapper has a potential of being one of the most valuable sources of choice food fish in the Gulf. Recent exploratory work with long lines off the Texas coast at 100 to 200 fathoms, revealed a promising stock of tile fish, a species not considered before as a potential resource of food fish. These species will be prime target for a food fish trawling program to be conducted around the Gulf at about 50-200 fathoms using the research vessel OREGON II.

Spanish Mackerel

At present this species is the subject of offshore aerial photographic reconnaissance for seasonal occurrence of schools. From this will evolve a preliminary estimate of available stock and a harvesting program. This program involves also the occurrence of offshore surface schooling tunas.

Calico Scallops

Discovered in commercial abundance in the northeastern Gulf some ten years ago, calico scallops as a fishery of significance never developed. Most productive grounds apparently are between Mobile and Apalachicola in about 10 to 25 fathoms. Because of renewed interest in scallop fishing, the Pascagoula Exploratory Fishing Base plans a reassessment of the beds.

Possibilities of mid-water trawling in the Gulf have not been thoroughly investigated and the Pascagoula Base plans to resume these explorations with R/V OREGON II.

Two harvesting projects are in the thinking and planning stage now. One is an automated unmanned fishing platform to catch and process industrial fish. The other is an electrified surface trawl (for pelagic species) operated by two vessels, with the cod end of the trawl emptying into a third vessel.

Shrimp Resources in the Gulf

Of the established fishery resources, the most important is shrimp. Our Bureau's main efforts are directed to this resource, with headquarters at our Biological Laboratory here in Galveston. The lines of research are so numerous and diversified that I can do little more than mention each briefly.

Gulf Oceanography

This program is concerned with the physical and chemical environment of the continental shelf and slope, and the oceanographic and atmospheric processes that influence this environment in the Gulf of Mexico. It will provide fishery biologists with details of the natural marine environment to the extent that evaluations can be made of those properties fundamental to the distribution and abundance of shrimp and fish populations. The ultimate objective is to devise a practical means of forecasting short or long term environmental deviations that effectively modify the size of the annual shrimp crop and the harvest of other fishery resources.

Of special interest is a project to explore utility of space technology and fisheries oceanography.

Estuarine Studies

The physical alteration and destruction of natural habitats in estuaries along the Gulf of Mexico are proceeding at an ever-increasing rate. The effects of the modifications of estuaries on fishery resources are not predictable because specific cause and effect relations are not known. It is clear that an evaluation of these coastal environments, pertaining to the life history, food change, and nursery grounds of shrimp and other marine species, is imperative to the conservation of commercial fisheries.

Major objectives of the program are to determine the value of various habitat types as related to fishery production, document the effects of specific types of construction on the estuarine environment, develop techniques for managing estuarine habitats for increased fishery reproduction, and assure that coastal fishery resources receive adequate protection from water development projects.

In addition to the estuarine studies conducted in the Galveston laboratory, similar studies in the eastern Gulf are underway at the Bureau's St. Petersburg Beach, Florida, Biological Laboratory.

Shrimp Population Dynamics

The goal of studies related to shrimp population dynamics is to formulate recommendations that can be incorporated into a program for managing shrimp resources in the Gulf of Mexico. To achieve this objective, it is necessary to determine the effect that fishing has on the population level and to understand how various management procedures influence yields from available stocks of shrimp.

Our research includes mark-recapture experiments on brown, white, and pink shrimp to determine growth, mortality, and movement; and studies to examine and define interrelations of the density of post larval shrimp, the abundance of juveniles and the size of the crop of adults available to the commercial fisheries.

Shrimp Aquaculture

A very important program which is now well underway at our Galveston laboratory is shrimp aquaculture. The rapid growth rate and the high economic value of shrimp has led to considerable interest in the possibility of pond-type shrimp culture, using low cost marginal areas. The success of economically growing shrimp in ponds devoid of predators depends on maintaining a supply of shrimp capable of obtaining maturity, mating, and spawning under artificial conditions. Our Galveston laboratory has been successful in rearing post larvae of brown and white shrimp, hatched in the laboratory to late juveniles in their man-made ponds.

Research now underway is designed to determine the feasibility of culturing shrimp economically under semi-natural conditions, to determine the importance of ecological factors which affect the growth and survival of shrimp in ponds, to develop methods of controlling or modifying environmental factors to insure maximum production of shrimp food, and to determine and create conditions essential for mating and spawning under laboratory conditions.

Pompano Ponds

Similar work relating to raising pompanos in ponds for commercial use is conducted at the Bureau's Biological Laboratory in St. Petersburg Beach, Florida.

Menhaden Resources in the Gulf

The menhaden fishery in the Gulf of Mexico is second in importance after shrimp. This has been a fairly recent development resulting in part from such industry innovations as aerial spotting of fish schools and mechanized net handling. There is concern both by industry and by government, as to whether the resource can sustain such exploitation without suffering damage that would eventually cripple the fishery.

Atlantic menhaden are closely related to those in the Gulf and have been under study at our Beaufort, North Carolina, Biological Laboratory since 1955. That program was expanded to include the Gulf resource in 1964.

Biological data are being collected from the commercial catch and estimates are being made of juvenile abundance in the estuaries. The problems of designing a large scale menhaden tagging program to industrial migrations, population structure, growth, and mortality have been worked out for Atlantic menhaden with a tagging of almost 400,000 last year. Hopefully, a similar project will soon be launched in the Gulf.

OTHER BCF GULF PROGRAMS

An extensive program on the effects of pesticides on a wide variety of marine organisms is conducted at the Bureau's Biological Laboratory in Gulf Breeze, Florida. These include determinations of the acute toxicity of the most widely used pesticides to estuarine fauna, chronic effect of long continued, low-level pesticide pollution on pilot sized eco systems, effects of pesticides on the behavior of the estuarine fauna; and effects of a large number of pesticides on invertebrates and fish. In addition, a pesticide monitoring program has been established with about fourteen coastal states cooperating in the work.

The Technology Laboratory at Pascagoula, Mississippi, serves the Bureau's Region 2 (South Atlantic and Gulf) and conducts several programs dealing with the determination of the biochemical composition of the commercially important seafoods of the region, the effect of various methods of storage and processing in relation to changes in quality of shrimp, crab, and other seafoods, effect of bacterially induced changes in biochemical constituents, and the consequent effect on quality, and a large variety of other problems as they may arise.

Through the Commercial Fisheries Research & Development Act, administered by the Bureau of Commercial Fisheries, we have an interest in a wide variety of programs being conducted by all the states bordering the Gulf of Mexico on a matching fund basis.

Through contract research our Galveston Biological Laboratory has projects dealing with post larval and juvenile pink shrimp with the University of Miami, Institute of Marine Science, and on white, brown and pink shrimp for the University of Southwestern Louisiana.

To supplement the oceanographic and biological programs, the Bureau conducts an extensive statistical program on fishery catch, effort and production, with headquarters in New Orleans and agents stationed at intervals from Brownsville, Texas, to southern Florida.

While not possibly classified as research, the Bureau operates a number of special service programs. These include a marketing program, seafood inspection, loans and grants, and market news.

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REVISION OF THE FLATFISH GENUS *TRICHOPSETTA* (BOTHIDAE) WITH DESCRIPTIONS OF THREE NEW SPECIES

WILLIAM W. ANDERSON AND ELMER J. GUTHERZ

REVISION OF THE FLATFISH GENUS *TRICHOPSETTA* (BOTHIDAE) WITH DESCRIPTIONS OF THREE NEW SPECIES[1]

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ABSTRACT

Three new species of flatfish, *Trichopsetta caribbaea, T. melasma,* and *T. orbisulcus,* are described. The only previously known species, *T. ventralis,* is redescribed. A terse description, relationship, range, illustration, and radiograph are provided for each species. Species of this genus are limited to the western North Atlantic from southern United States through the Caribbean to Surinam in depths of between 20 and 150 fathoms. A key is included for identifying species of this genus.

INTRODUCTION

Three new species were included in materials of the flatfish genus *Trichopsetta* collected by the Bureau of Commercial Fisheries exploratory fishing vessels OREGON and SILVER BAY. Specimens were collected off the southeastern United States, off the Bahama Islands, in the Gulf of Mexico and Caribbean Sea, and off the northern coast of South America as far east as Surinam (Fig. 1). This paper redefines the genus, describes the three new species in comparison with the only previously known species, *Trichopsetta ventralis* (Goode and Bean), and provides a key to all four species. Species of this genus are limited to the western North Atlantic Ocean, from southern United States through the Caribbean Sea to Surinam in depths between about 20 and 150 fathoms.

ABBREVIATIONS

The abbreviations used for the names of museums are as follows:

USNM — United States National Museum
MCZ — Museum of Comparative Zoology, Harvard
FMNH — Field Museum of Natural History, Chicago
SU — Stanford University Natural History Museum
ANSP — Academy of Natural Sciences of Philadelphia
LACM — Los Angeles County Museum of Natural History
BMNH — British Museum of Natural History, London
MNHM — Muséum National d'Histoire Naturelle, Paris
TABL — U. S. Bureau of Commercial Fisheries Tropical Atlantic Biological Laboratory, Miami.

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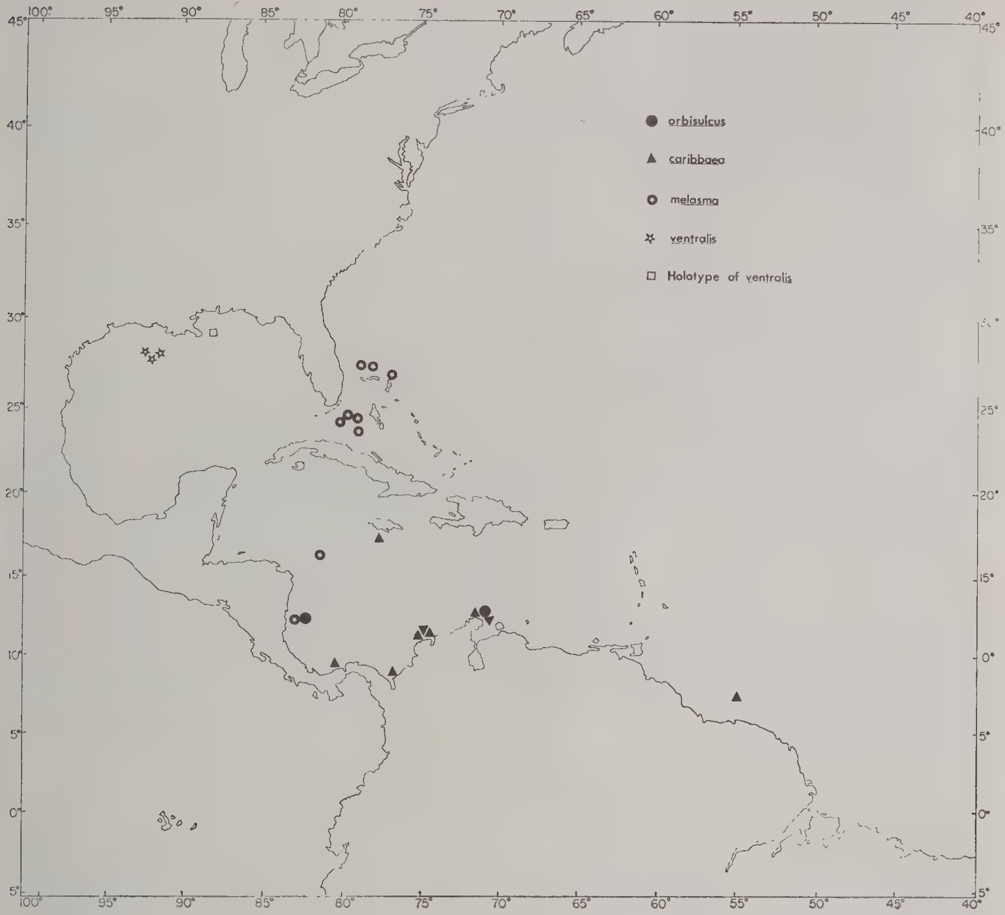
● orbisulcus
▲ caribbaea
○ melasma
☆ ventralis
□ Holotype of ventralis
100°
95°
90°
85°
80°
75°
70°
65°
60°
55°
50°
45°
40°
45°
40°
35°
30°
25°
20°
15°
10°
5°
0°
5°

FIGURE 1. Locations of capture of study specimens of the four species of *Trichopsetta,* and locality for holotype of *T. ventralis* (Goode & Bean).

MEASUREMENTS AND COUNTS

Measurements were taken on the ocular side unless otherwise indicated. The terms used are defined below.

1. Standard length—Tip of snout to end of hypural plate, on blind side.
2. Head length—Tip of snout to posteriormost point of fleshy margin of opercle.
3. Body depth—Greatest vertical measurement, excluding fin rays.
4. Eye diameter (upper)—Horizontal distance across eye, not a measurement of the orbit.
5. Pectoral-fin length—From base of first (anteriormost) pectoral ray to tip of longest ray.
6. Pelvic-fin length—From base of first pelvic ray to tip of longest ray.
7. Upper-jaw length—Anterior edge of premaxillary to posterior edge of maxillary.
8. Dorsal- and anal-fin rays—Counts recorded as total number of rays.

9. Gill rakers—Counts recorded for lower limb of first arch, including rudiments (no gill rakers occur on the upper limb).
10. Scales in lateral line—Number in lateral line from above point of connection of opercular membrane with body to end of hypural plate.
11. Vertebrae—Counts recorded as abdominal and caudal (the first caudal vertebra has its enlarged hemal spine in contact with the first pterygiophore of the anal fin).

Trichopsetta

Trichopsetta Gill, 1889: 601 (type-species *Citharichthys ventralis*, Goode & Bean, 1885, by monotypy).—Jordan & Evermann, 1898: 2669 (description).—Norman, 1934: 160 (description).

Sinistral; body ovate and compressed, depth less than ½ of standard length. Eyes about equal, separated by a narrow ridge; median groove may be present anteriorly. Mouth moderate, maxillary not extending beyond middle of lower eye. Jaws and dentition about equally developed on both sides; teeth small, conical, uniserial, and enlarged in front; vomer without teeth. Posterior nostril on blind side small, without membranous valve, close to anterior nostril; olfactory laminae few, arranged nearly parallel to each other, no central rachis. Gill rakers short and broad to moderately long and slender, not numerous; gill rakers absent on upper limb. Dorsal fin commencing behind and above posterior nostril of blind side, well in advance of upper eye; all rays simple. Pectoral fins unequal. Pelvic fins short based, that of the ocular side on median line and slightly in advance of that on blind side, six fin rays on each side. Caudal fin with 17 fin rays. Scales small, ctenoid on ocular side, cycloid on blind side. Ocular side of body scaled except for pectoral fin and its base, snout, interorbital, upper and lower jaws, and inter-radial membranes of fins; naked and scaled areas on blind side similar in extent to those on ocular side.

The general color pattern for preserved specimens is similar in all species. For this reason a statement of the color pattern is given here and is not repeated under the species discussions. Variations or color peculiar to a species are discussed under the species account. The color pattern consists of a brown or a tan (straw-colored) background with few to numerous spots or blotches on the body, median fins, and pelvic fin on ocular side. The background color and the number and intensity of spots or blotches vary greatly within and between species. Some color characteristics are common to all species: a dark spot on the body above the anterior edge of the cleithrum just anterior to the pectoral base; a small dark spot at the anterior end of the lateral line just above the point of connection of the opercular membrane. Most specimens of all species have: a series of spots on the body just under the dorsal fin and above the anal fin; a large blotch at the junction of the curved and straight portions of the lateral line and another on the lateral line just anterior to the caudal peduncle.

KEY TO THE SPECIES OF *Trichopsetta*

A. Gill rakers short and stout, 7 or 8 (including a rudiment) on lower limb of first arch; two furrows on head, one from anterior nostril on blind side to anterodorsal edge of upper orbit, the second just above anterior ⅓ of upper orbit; pectoral-fin length on blind side about 50 per cent that on ocular side .... *Trichopsetta orbisulcus*

AA. Gill rakers moderately long and slender, 9-11 (including rudiments) on lower limb of first arch; no furrows on head; pectoral-fin length on blind side either greater than on ocular side or exceeding 70 per cent the length on the ocular side.

B. Total scales in lateral line 84-94; pectoral fin on ocular side longer than on blind side; blind side dusky . *Trichopsetta melasma*

BB. Total scales in lateral line 63-79; pectoral fin on blind side longer than on ocular side; blind side immaculate.

C. Total scales in lateral line 63-68; dorsal-fin rays 89-95; anal-fin rays 69-75 .... *Trichopsetta ventralis*

CC. Total scales in lateral line 69-79; dorsal-fin rays 95-103; anal-fin rays 75-82 .... *Trichopsetta caribbaea*

Trichopsetta ventralis (Goode & Bean)

Figs. 2, 3

Citharichthys ventralis Goode & Bean, 1885: 592 (type description; locality ALBATROSS 2386, Gulf of Mexico off Mississippi delta, 29°15′N, 88°06′W, 60 fathoms).

Arnoglossus (?) *ventralis,* Jordan & Goss, 1889: 262 (distribution and taxonomic placement).

Trichopsetta ventralis, Gill, 1889: 601-602 (description).—Goode & Bean, 1896: 440 (description).—Jordan & Evermann, 1898: 2667 (description). —Norman, 1934: 160 (description).

Holotype.—USNM 37343: ALBATROSS station 2386, Gulf of Mexico off Mississippi Delta, 29°15′N, 88°06′W, 60 fathoms.

TABL Collections.—OREGON station 3795, 28°05.5′N, 92°38′W, 45-50 fathoms, 14 September, 1962 (5 males, 112 to 140 mm S.L.; 5 females, 77 to 110 mm S.L.); OREGON station 4727, 27°54′N, 92°04.5′W, 100 fathoms, 26 February, 1964 (2 males, 118 and 133 mm S.L.); OREGON station 4750, 27°55′N, 91°43′W, 100 fathoms, 6 March, 1964 (4 males, 126 to 142 mm S.L.); no data (one male, 124 mm S.L.; one female, 122 mm S.L.).

Diagnosis.—*Trichopsetta ventralis* can be distinguished from all other known species of the genus by the low number of scales in the lateral line.

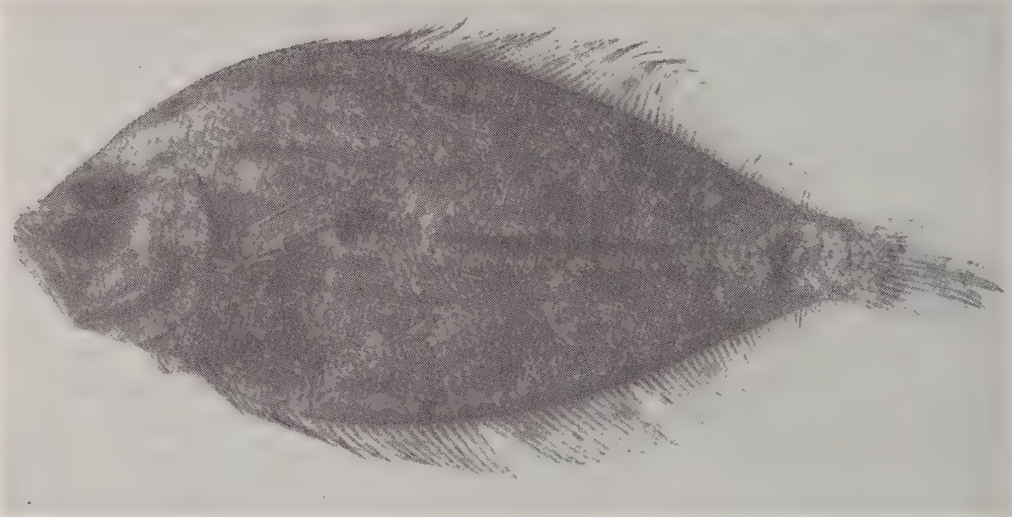

FIGURE 2. *Trichopsetta ventralis* (Goode & Bean), male, 140 mm S.L., OREGON station 4950.

It is also distinct from *T. orbisulcus* by the characters exclusive to that species (see section below, for diagnostic features of *T. orbisulcus*), and from *T. melasma* and most specimens of *T. caribbaea* by the lower number of dorsal- and anal-fin rays.

Description.—Counts and measurements of the study material for this species are given in Table 1, selected comparative counts for the four species in Table 2, and the range of selected body measurements (as per cent of standard length) for the four species in Table 3. A radiograph of a large specimen is shown in Figure 3.

The body is ovate, with the greatest depth about 42 to 49 per cent of the standard length. The head is deeply notched before the upper eye. The snout is blunt; the mouth is moderate, with the maxillary reaching a vertical through approximately the middle of the pupil of the lower eye. The upper jaw is about 40 to 42 per cent of the head length. The males lack well-developed spines on the head. The males have greatly elongated pelvic-fin rays on the blind side.

Color.—The basic color pattern is as given in the generic description. *T. ventralis* has a brown background with limited speckling and spots on the body and fins. The blotches at the junction of the straight and curved portions of the lateral line and near the base of the caudal fin are weak or missing in some specimens. Most males have a dark blotch on the anal fin between about the 4th and the 8th or 10th anal ray; this spot is weak or absent in some specimens. The blind side is immaculate.

TABLE 1
SELECTED PROPORTIONAL MEASUREMENTS AND COUNTS OF *Trichopsetta ventralis*

	OREGON station number																	
	3795 ♂	3795 ♂	4727 ♂	No data ♂	4750 ♂	4750 ♂	4727 ♂	3795 ♂	3795 ♂	3795 ♂	4750 ♂	4750 ♂	3795 ♀	3795 ♀	3795 ♀	3795 ♀	3795 ♀	No data ♀
Standard length (mm)	112	118	118	124	126	132	133	136	138	140	140	142	77	89	96	107	119	122
Head length (mm)	29.2	32.6	32.0	33.4	34.2	36.8	36.5	37.0	39.0	37.6	36.0	38.2	21.6	26.1	26.8	29.0	31.7	32.5
Body depth (mm)	49.5	52.2	51.3	60.2	55.3	57.7	56.1	65.0	66.0	63.7	63.7	68.3	32.5	37.4	40.0	47.0	51.7	58.4
Measurements (as per cent of standard length)																		
Head length	26.1	27.6	27.1	26.9	27.1	27.9	27.4	27.2	28.3	26.9	25.7	26.9	28.1	29.3	27.9	27.1	26.6	26.6
Body depth	44.2	44.2	43.5	48.5	43.9	43.7	42.2	47.8	47.8	45.5	45.5	48.1	42.2	42.0	41.7	43.9	43.4	47.9
Eye diameter (upper)	6.7	6.9	6.7	6.7	6.7	7.3	6.6	6.6	6.5	6.8	6.1	5.7	6.9	7.3	6.9	6.7	6.6	6.1
Pectoral fin																		
blind side	29.8	27.4	27.3	21.7	26.7	26.7	24.1	26.8	28.6	31.0	31.1	22.5	–	23.3	19.2	–	25.8	21.6
ocular side	18.8	18.1	17.4	18.6	18.4	–	17.4	19.3	20.4	18.6	18.0	17.6	18.7	18.5	17.3	18.4	18.0	18.0
Pelvic fin																		
blind side	31.5	33.5	27.5	32.8	31.8	31.9	31.0	31.6	35.7	34.9	35.7	33.1	14.0	11.5	12.3	12.1	12.6	12.4
ocular side	12.4	11.9	11.8	12.5	11.5	10.6	11.7	12.4	14.2	12.6	11.8	11.5	10.8	12.6	11.1	11.9	11.9	11.5
Counts																		
Scales in lateral line	66	68	64	67	67	65	63	64	65	66	68	67	64	67	67	63	63	66
Dorsal-fin rays	94	93	92	93	89	90	91	90	92	94	93	89	89	90	93	95	93	89
Anal-fin rays	75	72	74	73	71	71	73	69	72	73	75	72	70	70	71	73	74	69
Gill rakers lower limb	10	11	11	10	11	10	9	10	11	9	10	10	9	10	10	10	10	10
Pectoral-fin rays																		
blind side	10	8	8	8	7	7	8	7	9	9	8	8	–	8	7	7	7	8
ocular side	13	12	12	12	12	12	13	12	13	12	12	12	12	12	12	12	–	12

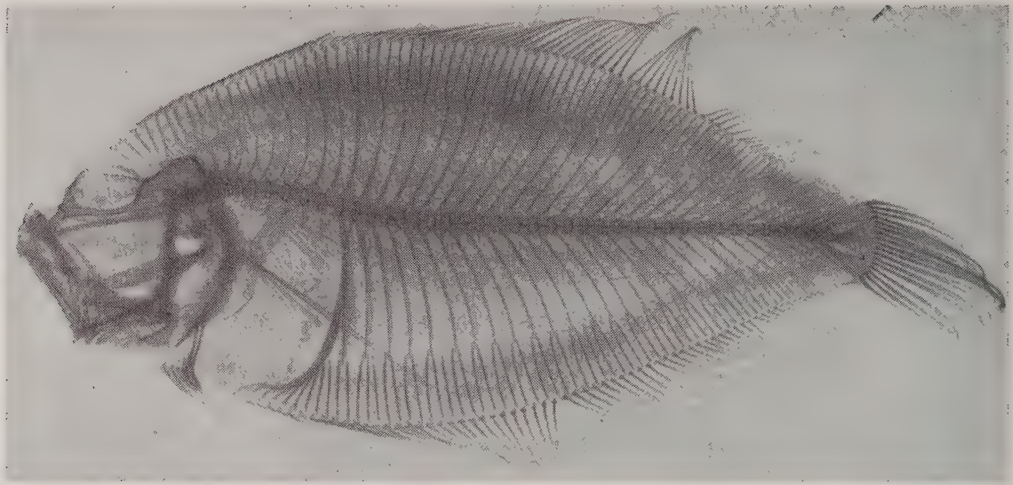

FIGURE 3. *Trichopsetta ventralis* (Goode & Bean), radiograph of male, 140 mm S.L., OREGON station 4950.

Relationships.—*Trichopsetta ventralis* is closest to *T. caribbaea* in the number of scales in the lateral line, but closest to *T. orbisulcus* in the numbers of dorsal- and anal-fin rays and vertebrae. *T. ventralis* and *T. caribbaea* are both immaculate on the blind side and the pectoral fin of the blind side is always the longer.

Range.—All specimens are from the northern Gulf of Mexico, near the type locality (ALBATROSS station 2386, 29°15′N, 88°06′W, in 60 fathoms). Hildebrand (1954), in a survey of the fauna of the brown shrimp grounds in the western Gulf of Mexico, recorded *Trichopsetta ventralis* from the shrimp grounds of south Texas and from the 24-10 grounds along the northern coast of Mexico. The 24-10 grounds extend, according to Hildebrand (1954: 245) "from about 20 miles below the Rio Grande to northeast of Sugarloaf Mountain at approximately 23°15′N." Hildebrand commented, "This distinctive flatfish was found only along the seaward edge of the present brown shrimp fishery. There may be a small shoreward movement during the spring, as it was taken in 18-24 fathoms during April and June and it was not taken during December and January in approximately the same locality." The species was not taken in trawl hauls made in 14-20 fathoms in the southern Gulf of Mexico off Álvaro Obregón in the Gulf of Campeche.

Trichopsetta caribbaea, new species

Figs. 4, 5

Holotype.—USNM 200414: OREGON station 3548, off south coast of Jamaica, 17°53′N, 77°56′W, 150 fathoms, 16 May, 1962 (male, 156 mm S.L.).

Paratypes.—USNM 200415: Oregon station 3548, off south coast of Jamaica, 17°53′N, 77°56′W, 150 fathoms, 16 May, 1962 (male, 147 mm S.L., collected with the holotype). USNM 200417: Oregon station 3587, off Panamá, 9°18′N, 80°25′W, 75 fathoms, 29 May, 1962 (one male, 104 mm S.L.; 5 females, 84 to 123 mm S.L.). USNM 200416: Oregon station 4843, off Colombia, 11°08.5′N, 74°29′W, 100-120 fathoms, 17 May, 1964 (2 males, 98 and 109 mm S.L.; 4 females, 96 to 116 mm S.L.). FMNH 66830: (one male, 86 mm S.L.; one female, 91 mm S.L.). MNHN 1966-737: (one male, 87 mm S.L.; one female, 100 mm S.L.). BMNH 1966.6.13.1-2: (one male, 93 mm S.L.; one female, 104 mm S.L.). MCZ 44911: (one male, 95 mm S.L.; one female, 122 mm S.L.). SU 63561: (one female, 80 mm S.L.). Oregon station 4844, off Colombia, 11°06.7′N, 74°30′W, 100 fathoms, 17 May, 1964. ANSP 103614: (one male, 93 mm S.L.; one female, 112 mm S.L.). LACM 6916-1: (one female, 117 mm S.L.). Oregon station 4856, off Colombia, 11°08′N, 74°23.8′W, 100 fathoms, 19 May, 1964. TABL Collection: Oregon station 4304, off Surinam, 7°30′N, 55°00′W, 100 fathoms, 24 March, 1963 (one male, 125 mm S.L.; 3 females, 131 to 150 mm S.L.); Oregon station 4391, off Colombia, 12°33′N, 71°09′W, 40 fathoms, 25 September, 1963 (one male, 130 mm S.L.; one female, 140 mm S.L.); Oregon station 4394, off Colombia, 12°37′N, 71°10′W, 65 fathoms, 25 September, 1963 (one female, 109 mm S.L.); Oregon station 4846, off Colombia, 11°06.8′N, 74°23.6′W, 50 fathoms, 17 May, 1964 (3 males, 90 to 111 mm S.L.; 3 females, 84 to 94 mm S.L.); Oregon station 4852, off Colombia, 11°07′N, 74°26′W, 60-65 fathoms, 18 May, 1964 (5 males, 86 to 99 mm S.L.; one female, 100 mm S.L.; 2 males or females, 74 and 81 mm S.L.); Oregon station 4857, off Colombia, 11°07′N, 74°21.5′W, 40-50 fathoms, 19 May, 1964 (3 males, 85 to 93 mm S.L.; 3 females, 87 to 110 mm S.L.; 1 male or female, 56 mm S.L.); Oregon station 4872, off Colombia, 11°01.8′N, 75°14′W, 35 fathoms, 23 May, 1964 (2 males, 98 and 134 mm S.L.; 4 females, 113 to 132 mm S.L.); Oregon station 4898, off Colombia, 08°53.8′N, 76°51.6′W, 100 fathoms, 27 May, 1964 (3 females, 73 to 96 mm S.L.).

Diagnosis.—*Trichopsetta caribbaea* is distinguished from the other members of the genus only by a combination of characters. It differs from *T. orbisulcus* (in addition to the characters exclusive to that species) in having more vertebrae and dorsal- and anal-fin rays, from *T. ventralis* in having more scales in the lateral line and (in most specimens) more dorsal- and anal-fin rays, and from *T. melasma* in having fewer scales in the lateral line and in having the longer pectoral fin on the blind side.

Description.—Counts and measurements of the holotype and 20 paratypes are given in Table 4, selected comparative counts for the four species in

TABLE 2
SELECTED COMPARATIVE COUNTS FOR THE FOUR SPECIES OF *Trichopsetta*

	Total number of scales in lateral line																															
	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94
T. ventralis	3	3	2	3	5	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
T. caribbaea	–	–	–	–	–	–	1	5	10	11	10	14	3	2	2	1	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
T. melasma	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1	2	2	1	2	2	2	1	1
T. orbisulcus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–

	Dorsal-fin rays																Vertebrae*					
	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	10-30	10-31	10-32	10-33	11-31	11-32
T. ventralis	4	3	1	2	5	2	1	–	–	–	–	–	–	–	–	–	9	9	–	–	–	–
T. caribbaea	–	–	–	–	–	–	2	12	9	13	15	7	2	1	2	–	–	3	15	3	1	1
T. melasma	–	–	–	–	–	–	–	–	–	2	2	2	2	3	3	2	–	2	12	1	–	1
T. orbisulcus	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–

	Anal-fin rays																	Gill rakers on lower limb of first arch				
	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	7	8	9	10	11
T. ventralis	2	2	3	3	4	2	2	–	–	–	–	–	–	–	–	–	–	–	–	3	11	4
T. caribbaea	–	–	–	–	–	–	3	8	15	13	11	8	3	2	–	–	–	–	–	10	41	12
T. melasma	–	–	–	–	–	–	–	–	–	–	–	3	2	2	4	4	1	–	–	6	6	4
T. orbisulcus	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–

* Precaudal plus caudal vertebrae.

TABLE 3

RANGE OF MEASUREMENTS (AS PER CENT OF STANDARD LENGTH) IN THE FOUR SPECIES OF *Trichopsetta*

	ventralis		*caribbaea*		*melasma*		*orbisulcus*	
	♂	♀	♂	♀	♂	♀	♂	♀
Head length	25.7-28.3	26.6-29.3	25.8-29.0	27.5-29.7	23.2-26.1	24.9-28.6	24.8	25.5
Body depth	42.2-48.5	41.7-47.9	39.8-44.9	38.4-43.4	39.7-43.0	39.9-42.9	42.4	42.8
Eye diameter (upper)	5.7- 7.3	6.1- 7.3	6.3- 8.2	7.0- 8.5	6.3- 7.8	6.9- 8.5	6.9	7.3
Pectoral fin								
blind side	21.7-31.1	19.2-25.8	19.4-23.8	16.7-24.5	10.6-13.9	10.7-14.3	6.9	6.8
ocular side	17.4-20.4	17.3-18.7	12.0-18.1	16.1-18.3	13.3-16.0	14.0-14.9	13.6	13.4
Pelvic fin								
blind side	27.5-35.7	11.5-14.0	25.9-36.9	10.6-13.4	31.3-59.7	10.6-12.9	10.6	11.1
ocular side	10.6-14.2	10.8-12.6	10.8-12.5	9.9-12.9	10.3-11.8	9.8-11.4	11.6	10.9

TABLE 4

Selected Proportional Measurements and Counts of *Trichopsetta caribbaea* (Holotype and First 20 Paratypes Examined)

	Oregon station number										
	4872	3587	4304	4391	4872	3548	3548	3587	3587	3587	4394
	♂	♂	♂	♂	♂	♂	♂*	♀	♀	♀	♀
Standard length (mm)	98	104	125	130	134	147	156	84	91	98	109
Head length (mm)	26.9	29.0	36.3	35.8	38.6	40.1	40.3	23.8	25.6	28.2	30.8
Body depth (mm)	39.0	42.0	53.6	58.4	56.6	64.0	65.0	35.0	39.5	38.5	44.0
Measurements (as per cent of standard length)											
Head length	27.4	27.9	29.0	27.5	28.8	27.3	25.8	28.3	28.1	28.8	28.3
Body depth	39.8	40.4	42.9	44.9	42.2	43.5	41.7	41.7	43.4	39.3	40.4
Eye diameter (upper)	8.1	7.2	7.5	7.5	8.2	6.3	6.4	8.0	8.1	7.1	7.9
Pectoral fin:											
blind side	23.8	21.0	21.7	23.2	23.1	19.4	21.0	21.7	20.7	18.2	19.4
ocular side	15.9	16.5	12.0	16.5	18.1	16.7	16.3	17.7	16.5	16.1	16.5
Pelvic fin:											
blind side	25.9	26.7	31.0	31.4	36.2	36.9	35.6	11.4	11.2	10.6	11.0
ocular side	10.8	12.5	11.0	12.3	12.0	11.9	11.3	11.1	10.9	10.3	9.9
Counts											
Scales in lateral line	74	75	70	74	74	75	72	76	69	77	72
Dorsal-fin rays	102	98	97	97	98	99	98	99	97	100	100
Anal-fin rays	81	77	77	76	77	79	76	75	76	78	81
Gill rakers:											
lower limb	9	11	10	10	11	11	10	9	9	10	11
Pectoral-fin rays:											
blind side	7	8	7	8	8	7	8	8	8	7	8
ocular side	12	12	12	12	12	12	12	12	12	12	12

* Holotype.

Table 2, and range of selected body measurements (as per cent of standard length) for the four species in Table 3. A radiograph of the holotype is shown in Figure 5.

The body is ovate, with its greatest depth about 38 to 45 per cent of the standard length. The head is deeply notched before the upper eye. The snout is blunt; the mouth is moderate, with the maxillary usually reaching a vertical through the middle of the pupil of the lower eye. The upper jaw is about 39-43 per cent of the head length. The males lack

TABLE 4 (Continued)

	Oregon station number									
	4872 ♀	3587 ♀	3587 ♀	4872 ♀	4872 ♀	4304 ♀	4872 ♀	4304 ♀	4391 ♀	4304 ♀
Standard length (mm)	113	117	123	123	128	131	132	138	140	150
Head length (mm)	33.6	32.6	34.1	36.0	37.0	37.0	38.7	38.3	38.5	42.5
Body depth (mm)	46.2	50.5	50.7	47.2	52.2	51.6	55.3	56.0	57.5	60.1
Measurements (as per cent of standard length)										
Head length	29.7	27.9	27.7	29.3	28.9	28.2	29.3	27.8	27.5	28.3
Body depth	40.9	43.2	41.2	38.4	40.8	39.4	41.9	40.6	41.1	40.1
Eye diameter (upper)	8.5	7.4	7.6	7.3	7.8	7.0	7.6	7.2	7.6	7.3
Pectoral fin:										
blind side	22.9	21.4	24.5	16.7	–	20.9	21.8	22.9	–	21.0
ocular side	17.4	17.3	18.0	16.1	17.7	16.1	18.3	17.4	17.1	17.3
Pelvic fin:										
blind side	12.5	12.3	12.2	10.8	12.1	11.1	13.1	11.6	13.4	11.7
ocular side	12.3	12.1	12.0	10.4	11.3	10.3	11.7	11.2	12.9	11.1
Counts										
Scales in lateral line	72	74	71	73	70	73	73	73	72	71
Dorsal-fin rays	98	99	95	98	96	99	97	100	96	98
Anal-fin rays	77	79	77	80	76	79	76	78	77	76
Gill rakers:										
lower limb	10	11	11	9	10	11	10	10	10	10
Pectoral-fin rays:										
blind side	8	7	8	8	8	7	8	8	8	8
ocular side	12	12	12	13	12	11	13	12	13	12

well-developed spines on the head, and have greatly elongated pelvic-fin rays on the blind side.

Color.—The basic color pattern is as given in the generic description. *T. caribbaea* has a background color varying from tan to brown, with few to numerous spots and blotches on the body and fins in addition to the basic pattern. A few males have a dark blotch on the anterior rays of the anal fin. Usually a pair of faint spots is present on the caudal rays near the base of the fin. The blotches at the junction of the straight and curved portions of the lateral line and on the lateral line near the caudal peduncle are distinct on some specimens, but are diffuse or absent on others. The blind side is immaculate.

Relationships.—*Trichopsetta caribbaea* is closest to *T. orbisulcus* in number of scales in the lateral line, but nearer *T. melasma* in numbers of

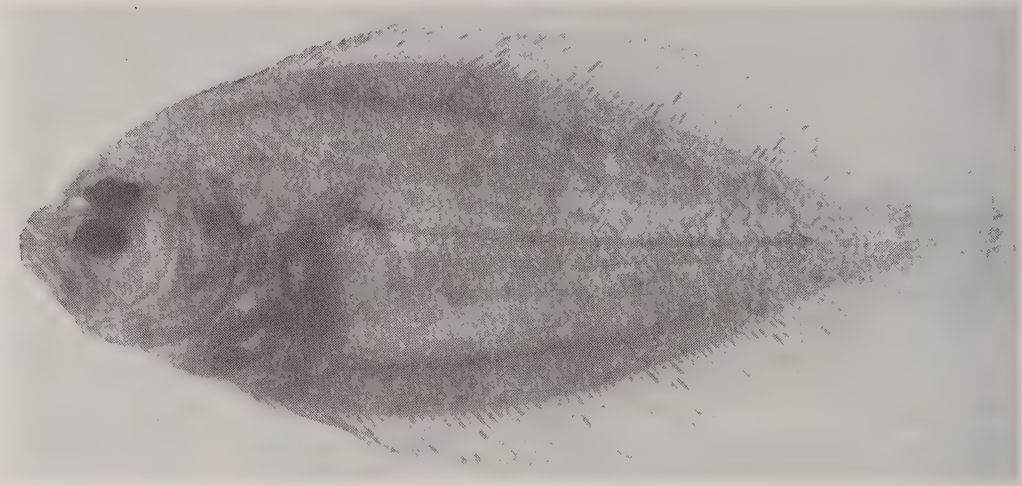

FIGURE 4. *Trichopsetta caribbaea,* holotype.

dorsal- and anal-fin rays. In the possession of a high number of vertebrae it agrees with *T. melasma,* as compared with the lower count in *T. orbisulcus* and *T. ventralis*. Both *T. caribbaea* and *T. ventralis* are immaculate on the blind side, and have the longer pectoral fin on the blind side.

Range.—In the Caribbean off Jamaica, Panamá, and Colombia in 35 to 150 fathoms; one catch from off Surinam in 100 fathoms.

Name.—This species is named *caribbaea* for the Caribbean Sea, where most of the specimens were collected.

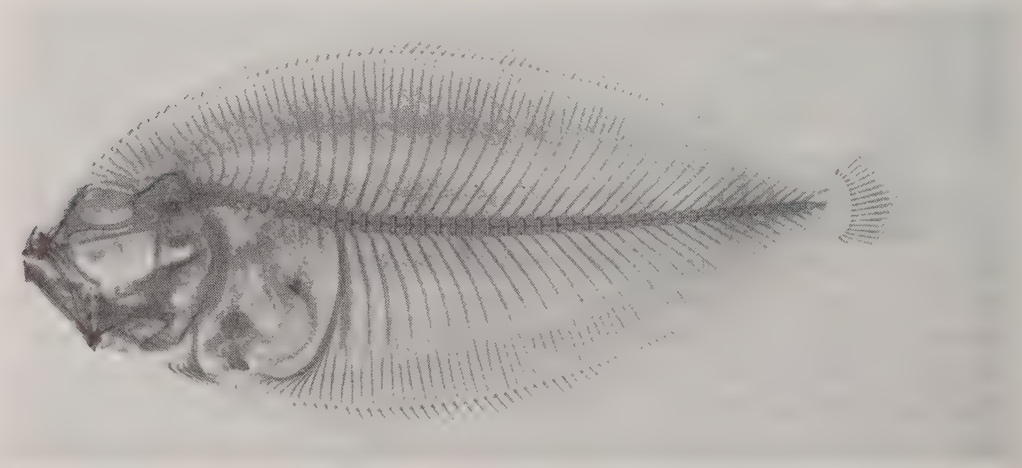

FIGURE 5. *Trichopsetta caribbaea,* radiograph of holotype.

TABLE 5

Selected Proportional Measurements and Counts of *Trichopsetta melasma*

	Oregon or Silver Bay station number															
	S.B. 2445 ♂	S.B. 3467 ♂	S.B. 3469 ♂	Ore. 3608 ♂	S.B. 2470 ♂	Ore. 3625 ♂	S.B. 2467 ♂*	S.B. 2471 ♂	S.B. 3469 ♀	Ore. 3577 ♀	S.B. 3467 ♀	S.B. 3476 ♀	Ore. 3625 ♀	S.B. 2471 ♀	Ore. 3625 ♀	Ore. 3625 ♀
Standard length (mm)	122	122.5	144.5	150	160.5	175	181	199	73	75.3	116.6	134	152	175	177	205
Head length (mm)	31.8	30.7	33.5	38.8	40.7	43.0	43.1	48.1	19.5	21.5	29.8	34.2	40.2	44.5	44.0	51.6
Body depth (mm)	52.0	48.8	59.2	59.6	65.8	74.5	77.8	83.0	30.2	30.5	50.0	53.5	65.2	71.4	76.0	82.0
Measurements (as per cent of standard length)																
Head length	26.1	25.1	23.2	25.9	25.4	24.6	23.8	24.2	26.7	28.6	25.6	25.5	26.4	25.4	24.9	25.2
Body length	42.6	39.8	41.0	39.7	41.0	42.6	43.0	41.7	41.4	40.5	42.9	39.9	42.9	40.8	42.9	40.0
Eye diameter (upper)	7.5	7.3	–	7.8	6.5	6.3	6.6	6.8	8.1	8.5	7.5	7.1	7.2	6.9	6.9	7.1
Pectoral fin																
blind side	13.9	10.6	–	11.5	13.1	12.2	11.8	10.6	13.2	14.3	11.0	11.9	11.1	12.0	11.2	10.7
ocular side	15.5	13.5	13.3	14.9	16.0	15.4	15.0	14.7	14.0	14.6	14.2	–	14.7	14.7	14.9	14.4
Pelvic fin																
blind side	34.7	31.3	34.7	59.7	42.6	53.4	47.6	52.5	11.0	12.9	10.6	11.2	11.4	–	11.9	10.8
ocular side	10.7	10.3	10.9	11.3	11.8	10.6	10.4	11.2	10.7	10.6	9.1	10.7	10.7	11.4	11.3	9.8
Counts																
Scales in lateral line	87	91	92	90	87	94	93	84	88	88	86	89	85	90	92	91
Dorsal-fin rays	99	101	100	103	103	100	102	102	98	101	99	102	98	103	104	104
Anal-fin rays	82	83	81	83	84	81	83	83	80	82	80	84	80	84	85	84
Gill rakers																
lower limb	9	11	11	11	9	11	10	9	9	10	10	10	9	10	9	10
Pectoral-fin rays																
blind side	9	8	10	8	9	9	7	9	9	8	10	8	9	9	8	9
ocular side	12	12	12	12	13	12	11	13	12	9	13	12	13	12	12	13

* Holotype.

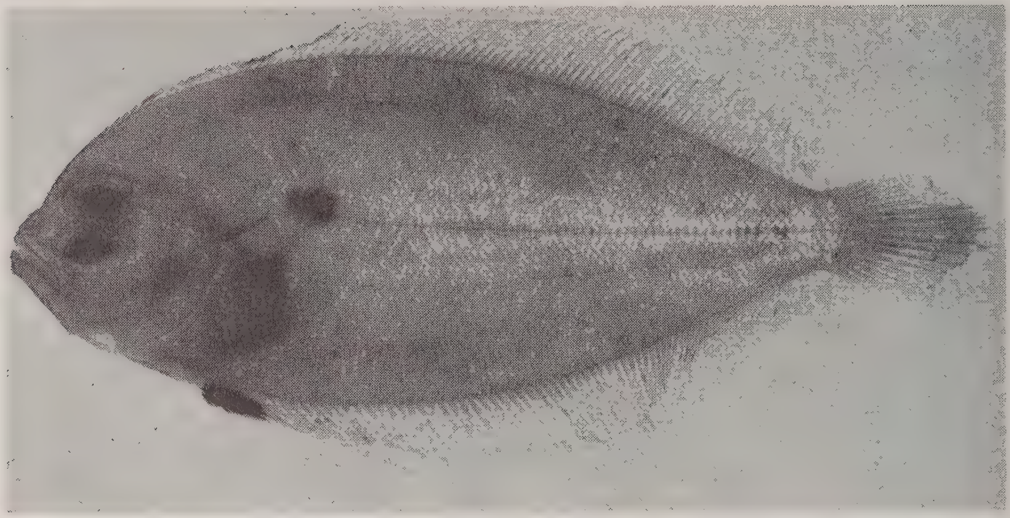

FIGURE 6. *Trichopsetta melasma,* holotype.

Trichopsetta melasma, new species

Figs. 6, 7

Holotype.—USNM 200418: SILVER BAY station 2467, Great Bahamas Bank off Andros Island, 23°40′N, 79°06′W, 125 fathoms, 6 November, 1960 (male, 181 mm S.L.).

Paratypes.—USNM 200420: SILVER BAY station 2445, Straits of Florida off Cay Sal Bank, 24°08′N, 80°08′W, 138 fathoms, 3 November, 1960 (one male, 122 mm S.L.). USNM 200421: SILVER BAY station 3476, off Great Abaco Island, 26°49′N, 77°01′W, 75 to 150 fathoms, 26 October, 1961 (one female, 134 mm S.L.). USNM 200419: OREGON station 3625, off Honduras, 16°26′N, 81°35′W, 120 fathoms, 6 June, 1962 (one female, 177 mm S.L.). MCZ 44912: SILVER BAY station 2470, off Andros Island and southern tip of Florida, 24°25′N, 79°13′W, 125 fathoms, 7 November, 1960 (one male, 160 mm S.L.). BMNH 1966.6.13.3: SILVER BAY station 2471, off Andros Island and southern tip of Florida, 24°34′N, 79°16′W, 150 fathoms, 7 November, 1960 (one male, 199 mm S.L.). SU 63562: SILVER BAY station 2471, off Andros Island and southern tip of Florida, 24°34′N, 79°16′W, 150 fathoms, 7 November, 1960 (one female, 175 mm S.L.). TABL Collection: SILVER BAY station 3467, north of Grand Bahama Island, 27°27′N, 79°00′W, 125-150 fathoms, 25 October, 1961 (one male, 122 mm S.L.; one female, 116 mm S.L.); SILVER BAY station 3469, north of Grand Bahama Island, 27°23′N, 78°35′W, 110 fathoms, 25 October, 1961 (one male, 144 mm S.L.; one female, 73 mm S.L.); OREGON station 3577, off Nicaragua, 12°32′N, 82°25′W, 85 fathoms, 23 May, 1962 (one female, 75 mm S.L.); OREGON station 3625, off Honduras, 16°26′N,

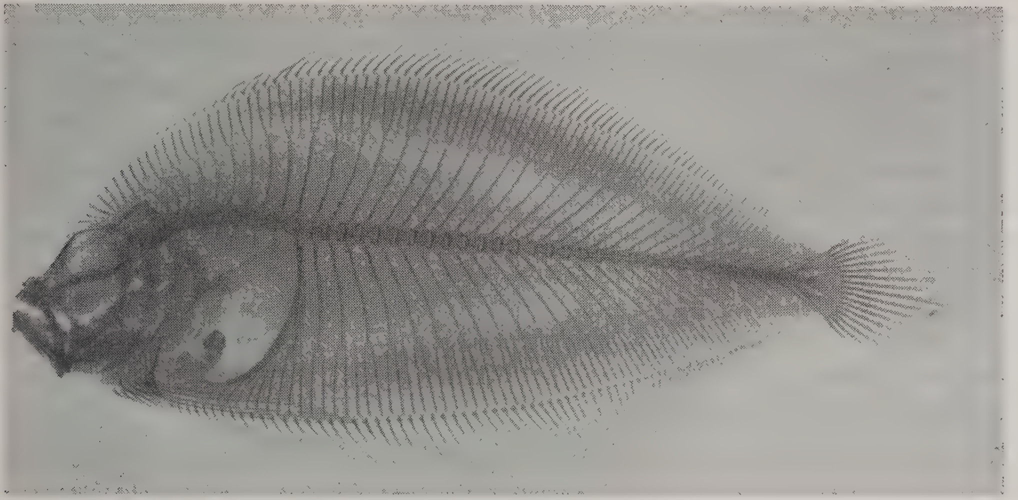

FIGURE 7. *Trichopsetta melasma,* radiograph of holotype.

81°35′W, 120 fathoms, 6 June, 1962 (one male, 175 mm S.L.; 2 females, 152 and 205 mm S.L.).

Diagnosis.—*Trichopsetta melasma* can be distinguished from the other species of the genus by the high number of scales in the lateral line. It is distinct also from *T. ventralis* and *T. orbisulcus* in having a higher number of dorsal- and anal-fin rays, and from *T. caribbaea* in having the longer pectoral fin on the ocular side.

Description.—The counts and measurements for the holotype and paratypes are given in Table 5, the selected comparative counts for the four species are in Table 2, and the ranges of selected body measurements (as per cent of standard length) for the four species are in Table 3. A radiograph of the holotype is shown in Figure 7.

The body is ovate, with its greatest depth about 39 to 43 per cent of the standard length. The head is deeply notched before the upper eye. The snout is blunt, the mouth moderate; the maxillary reaches a vertical through the anterior one-third to middle of the pupil of the lower eye. The upper jaw is about 37 to 41 per cent of the head length. The larger males have a well-developed symphyseal spine on the lower jaw, one on the snout above the upper lip, and on the anterior orbital rim of both eyes. The males have greatly elongated pelvic-fin rays on the blind side.

Color.—The basic color pattern is given in the generic description. *Trichopsetta melasma* tends to have a tan- or straw-colored background on the ocular side, and has fewer spots and blotches than do the other three species. The dark area at the junction of the straight and curved parts of the lateral line is more pronounced in *melasma* than it is in the other species; it appears more as a round spot than as a blotch. The males have a black spot on the anterior portion of the anal fin, usually between the first and seventh rays. The blind side has a straw-colored background and is dusky.

Relationships.—*Trichopsetta melasma* is closest to *T. caribbaea* in number of vertebrae and dorsal- and anal-fin rays. Although there is an overlap in the numbers of both dorsal- and anal-fin rays, *T. melasma* averages a larger number of rays in both fins. *Trichopsetta melasma, T. ventralis,* and *T. caribbaea* are alike in the numbers of gill rakers on the lower limb of the first arch. Both *Trichopsetta melasma* and *T. orbisulcus* are dusky on the blind side; they have longer pectoral fins on the ocular side and well-developed head spines in the males.

Range.—Known from off south Florida and north of the Bahamas, Florida Straits between Andros Island and tip of Florida, Honduras, and Nicaragua in 75 to 150 fathoms (usually over 100 fathoms).

Name.—This species is given the name *melasma,* in reference to the black spot on the anterior rays of the anal fin in male specimens.

Trichopsetta orbisulcus, new species

Figs. 8, 9

Holotype.—USNM 200422: Oregon station 4394, off western Venezuela, 12°37′N, 71°10′W, 65 fathoms, 25 September, 1963 (male, 116.6 mm S.L.).

Paratype.—TABL collection: Oregon station 3577, off Nicaragua, 12° 32′N, 82°25′W, 85 fathoms, 23 May, 1962 (female, 97.3 mm S.L.).

Diagnosis.—*Trichopsetta orbisulcus* is distinguished from the other species of the genus in having: (1) two furrows on the head, one from the anterior nostril of the blind side to the anterodorsal edge of the upper orbit, and the second one just above the dorsal edge of the anterior ⅓ of the upper orbit; (2) the gill rakers short and stout, with 7 or 8 (including a rudiment) on the lower limb of the first arch; (3) the pectoral-fin length on the blind side about 50 per cent of that on the ocular side; and (4) the male without elongated pelvic-fin rays on the blind side.

Description.—The counts and measurements of the holotype and paratype are given in Table 6, the selected comparative counts for the four species are in Table 2, and the range of selected body measurements (as per cent of standard length) for the four species are in Table 3. A radiograph of the holotype is shown in Figure 9.

The body is ovate, with its greatest depth about 43 per cent of the standard length. The head is not deeply notched before the upper eye as in the other three species, but the profile is broken where the furrow

TABLE 6
SELECTED PROPORTIONAL MEASUREMENTS AND COUNTS OF
Trichopsetta orbisulcus

	OREGON station numbers	
	4394 ♂ *	3577 ♀
Standard length (mm)	116.6	97.3
Head length (mm)	28.9	24.8
Body depth (mm)	49.4	41.6
Measurements (as per cent of standard length)		
Head length	24.8	25.5
Body depth	42.4	42.8
Eye diameter (upper)	6.9	7.3
Pectoral fin		
blind side	6.9	6.8
ocular side	13.6	13.4
Pelvic fin		
blind side	10.6	11.1
ocular side	11.6	10.9
Counts		
Scales in lateral line	78	80
Dorsal-fin rays	91	92
Anal-fin rays	70	73
Gill rakers		
lower limb	8	7
Pectoral-fin rays		
blind side	10	10
ocular side	12	12

* Holotype.

crosses from the upper eye on the ocular side to the anterior nostril on the blind side. The snout is blunt, the mouth moderate, with the maxillary reaching a vertical through the anterior edge of the pupil of the lower eye. The upper jaw is about 33 per cent of the head length. The male has a well-developed symphyseal spine on the lower jaw, one on the snout above the upper lip, and one on the anterior orbital rim of the lower eye.

Color.—The basic color pattern is given in the generic description. In *orbisulcus,* the furrows on the head are blackish, and the male has a large black spot on the dorsal fin between the 3rd and 7th rays. Markings on the ocular side of the pectoral fin form cross bars or bands on the distal part of the fin. The blind side is lightly dusky, more noticeably along the dorsal- and anal-fin bases on the posterior half of the body.

Relationships.—The genera *Trichopsetta* and *Engyophrys* are very closely

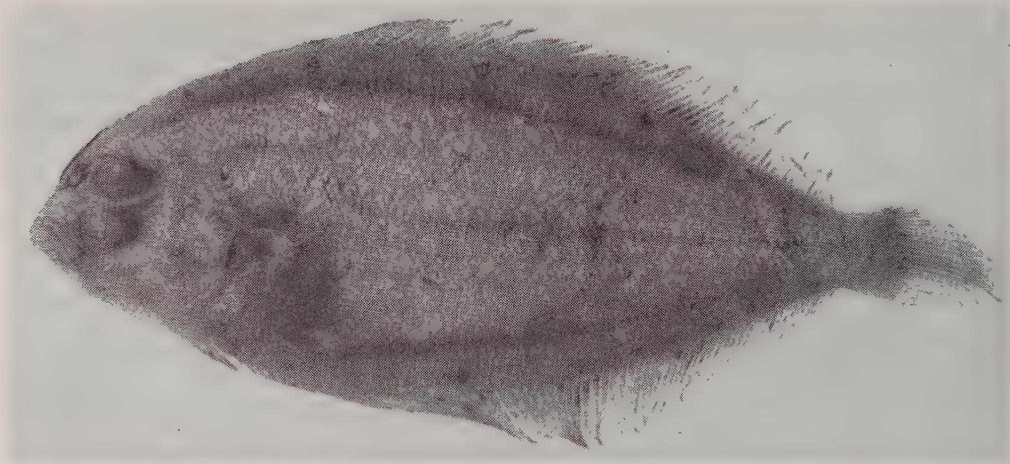

FIGURE 8. *Trichopsetta orbisulcus,* holotype.

related, and in some characters *T. orbisulcus* may be nearer to *Engyophrys* than to *Trichopsetta.* The males of the other three species of *Trichopsetta* all have some of the pelvic rays on the blind side greatly elongated, but *T. orbisulcus* and the known species of *Engyophrys* do not show this character. The shorter, heavier, and less numerous gill rakers on the lower limb of the first arch of *T. orbisulcus* approach the condition in *Engyophrys,* as opposed to the longer, more slender, and more numerous gill rakers in the other three species of *Trichopsetta.* However, the strong dentition in both blind and ocular sides of each of the two jaws, as well as the much larger mouth suggest a closer relationship to *Trichopsetta*; we place the species in this genus.

T. orbisulcus is closest to *T. ventralis* in numbers of vertebrae and dorsal- and anal-fin rays, but nearer to *T. caribbaea* in the total number of scales in the lateral line. The dusky color of the blind side and the presence in the males of a well-developed symphyseal spine on the lower jaw, on the snout above the upper lip, and on the orbital rim of one or both eyes, are shared only with *T. melasma.* Only in *T. orbisulcus* and *T. melasma* are the pectoral fins longer on the ocular side; in *orbisulcus* the pectorals of the blind side are only 50 per cent the length on the ocular side, whereas in *melasma* they are 70 per cent or more.

Range.—Known from only two specimens, one taken off Nicaragua in 85 fathoms, and the other off western Venezuela in 65 fathoms.

Name.—The name *orbisulcus* refers to the furrows on the head, above, and in front of, the upper eye (orbis = the orbit, and sulcus = a furrow).

ACKNOWLEDGMENTS

We thank Dr. James C. Tyler, of The Academy of Natural Sciences of

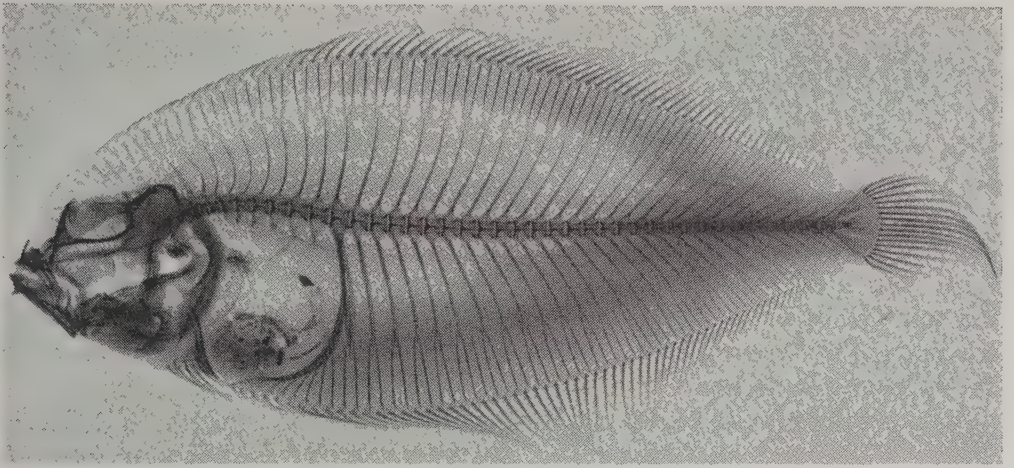

FIGURE 9. *Trichopsetta orbisulcus,* radiograph of holotype.

Philadelphia, for his thorough review of the manuscript. For their helpful suggestions on the manuscript we thank also: Dr. C. Richard Robins, Institute of Marine Sciences, University of Miami; and Frederick H. Berry and George C. Miller, U. S. Bureau of Commercial Fisheries Tropical Atlantic Biological Laboratory, Miami, Florida. We are indebted to Harvey R. Bullis, Jr., U. S. Bureau of Commercial Fisheries, Pascagoula, Mississippi, for the collection of specimens used in this study.

SUMMARY

The flatfish genus *Trichopsetta* has been redescribed and three new species added. Species of this genus are limited to the western North Atlantic Ocean, from the southern United States through the Caribbean to Surinam, in depths of 20 to 150 fathoms.

Descriptions, ranges, illustrations, and radiographs are given for the three new species and for the single previously known *Trichopsetta ventralis*. A key is included for identification of the four species.

T. orbisulcus can be distinguished from the other three species of *Trichopsetta* by the following characters: two furrows on the head, one anterior to the upper eye and the second above the upper eye; gill rakers, short and stout, 7-8; pectoral fin length on the blind side only about 50 per cent that of the ocular side. *T. melasma* can be separated from *T. ventralis* and *T. caribbaea* by the higher scale count of 84-94 (vs. 63-79), and by its possession of a longer pectoral fin on the ocular side than on the blind side. *T. ventralis* can be separated from *T. caribbaea* by the number of scales in the lateral line (63-68 vs. 69-79), the number of dorsal fin rays (89-95 vs. 95-103), and the number of anal fin rays (69-75 vs. 75-82).

SUMARIO

REVISION DEL GENERO DE PECES PLANOS *Trichopsetta* (BOTHIDAE), CON DESCRIPCIONES DE TRES NUEVAS ESPECIES

Se redescribe el género de peces planos *Trichopsetta* y se añaden tres nuevas especies. Las especies de este género están limitadas a la región occidental del Atlántico Norte, del sur de los Estados Unidos, a través del Caribe, hasta Surinam y a profundidades de 20 a 150 brazas.

Se dan descripciones, variaciones, ilustraciones y radiografías de las tres nuevas especies así como de la única especie que era previamente conocida, *Trichopsetta ventralis*. Se incluye una clave para la identificación de las cuatro especies.

T. orbisulcus puede ser distinguida de las otras tres especies de *Trichopsetta* por los siguientes caracteres: dos surcos en la cabeza, uno anterior al ojo superior y el segundo arriba de dicho ojo; 7-8 rastrillos branquiales cortos y gruesos; el largo de la aleta pectoral en el lado ciego alrededor de un 50 por ciento del de la del lado con ojos. *T. melasma* puede ser separada de *T. ventralis* y *T. caribbaea* por el mayor número de escamas (84-94 contra 63-79), y por la posesión de aletas pectorales más largas en el lado ocular que en el lado ciego. *T. ventralis* puede ser separada de *T. caribbaea* por el número de escamas en la línea lateral (63-68 contra 69-79), el número de radios de la aleta dorsal (89-95 contra 95-103), y el número de radios de la aleta anal (69-75 contra 75-82).

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Interaction of Gamma Irradiation and Salinity on Respiration of Brine Shrimp (*Artemia salina*) Nauplii

J. W. ANGELOVIC AND D. W. ENGEL

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RADIATION RESEARCH **35,** 102–108 (1968)

Interaction of Gamma Irradiation and Salinity on Respiration of Brine Shrimp (*Artemia salina*) Nauplii[1]

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Angelovic, J. W., and Engel, D. W. Interaction of Gamma Irradiation and Salinity on Respiration of Brine Shrimp (*Artemia salina*) Nauplii. *Radiation Res.* **35,** 102–108 (1968).

Respiration rates and Q_{10}'s of 1-day-old brine shrimp nauplii were affected significantly by radiation, the salinity of the water, and the interaction between the two factors. Respiration rates were measured in salinities from 5 to 200‰. Irradiated nauplii received doses of ^{60}Co radiation of 10,000 to 80,000 rads. In general, respiration rates of irradiated nauplii were significantly lower than those of unirradiated nauplii at salinities of 5, 50, and 200‰, but were higher at 100 and 150‰. When nauplii were in the highest salinity, 200‰, each increase in radiation above 10,000 rads caused a corresponding decrease in the rate of respiration. Similarly, at each salinity the nauplii exposed to the highest radiation dose, 80,000 rads, had the lowest rate of respiration. The highest levels of radiation and salinity acted synergistically and depressed the respiration rate to the lowest point. The greatest effect on Q_{10}'s was at the highest salinity. At this salinity, Q_{10} values for all irradiated nauplii were significantly lower than for controls or for irradiated nauplii at other salinities.

INTRODUCTION

Ionizing radiation and salinity both influence the physiological activity of marine species. Although the effects of these factors have frequently been tested individually on organisms, their interaction has been considered in only a few studies. The ability of irradiated and unirradiated juveniles of the silver salmon, *Oncorhynchus kisutch*, to migrate from fresh water to the sea was affected by the interaction of radiation and salinity (*1*). Angelovic *et al.* (*2*) demonstrated that radiation and salinity interacted to affect the survival of the mudminnow, *Fundulus heteroclitus*, the grass

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[1] This research was supported through a cooperative agreement between the U. S. Fish and Wildlife Service and the U. S. Atomic Energy Commission.

shrimp, *Palaemonetes pugio*, and the brine shrimp, *Artemia salina*, and Neuhold and Sharma (*3*) found that the two factors interacted to affect survival of the rainbow trout, *Salmo gairdneri*. The loss of ^{22}Na by the mudminnow, *Fundulus heteroclitus*, also was affected by the interaction of radiation and salinity (*4*).

We examined the effects of salinity, radiation, and their interaction on metabolism in 1-day-old nauplii of the brine shrimp, *Artemia salina*. Brine shrimp were chosen because they naturally tolerate a very wide range of salinities and are relatively resistant to radiation. The early nauplius stage was used to minimize differences in respiration rates due to size variation and stage of development. The effect of radiation and salinity on the brine shrimp was measured by changes in the respiratory metabolism (both Q_{O_2} and Q_{10}) of the nauplii.

MATERIALS AND METHODS

Brine shrimp from Great Salt Lake, which has a salinity of 220‰ (parts per thousand), were used throughout the experiments. Nauplii were hatched in 30‰ sea water at room temperature (22°C) and transferred soon after hatching to one of five salinities—5, 50, 100, 150, or 200‰. All sea water solutions were made from an artificial sea salt mixture. After overnight acclimation to the desired salinity, the 1-day-old nauplii were exposed to doses of 10,000, 20,000, 40,000, or 80,000 rads of ^{60}Co radiation. Radiation was administered at a rate of 365 rads/min ± 10% at room temperature and with continuous aeration. Controls were treated similarly except for irradiation.

Respiration was measured during the first 4 hours after irradiation on a differential respirometer. Each flask contained the animals present in 3 ml of water taken from a dense population of nauplii plus 0.5 ml of 20% KOH in the side arm. During respiration determinations the flasks were shaken 80 times per minute and maintained at 20°C. Respiration rates (Q_{O_2} values) were calculated as microliters of O_2 per milligram of dry weight per hour. Respiration rates at temperatures of 20° and 30°C were used to obtain Q_{10} values. The Q_{10} values were calculated without using Q_{O_2} values for any intermediate temperatures because respiration rates of brine shrimp nauplii have a linear relation to temperature between 20° and 30°C (Engel and Angelovic, unpublished data). Analyses of variance were calculated to determine the significance of the main effects and the interaction of radiation and salinity on Q_{O_2} and Q_{10} values. Duncan's multiple range test was used to test for significant differences between mean values. In the following text all reported changes or differences between Q_{O_2}'s or Q_{10}'s at different combinations of salinity and radiation dose are statistically significant at the 5% probability level or less.

Effect of Salinity and Radiation on Respiration Rates

Measurements of respiration rates (Q_{O_2}) at 20°C show that salinity affected the respiration rates of both control and irradiated brine shrimp nauplii (Fig. 1). Mean

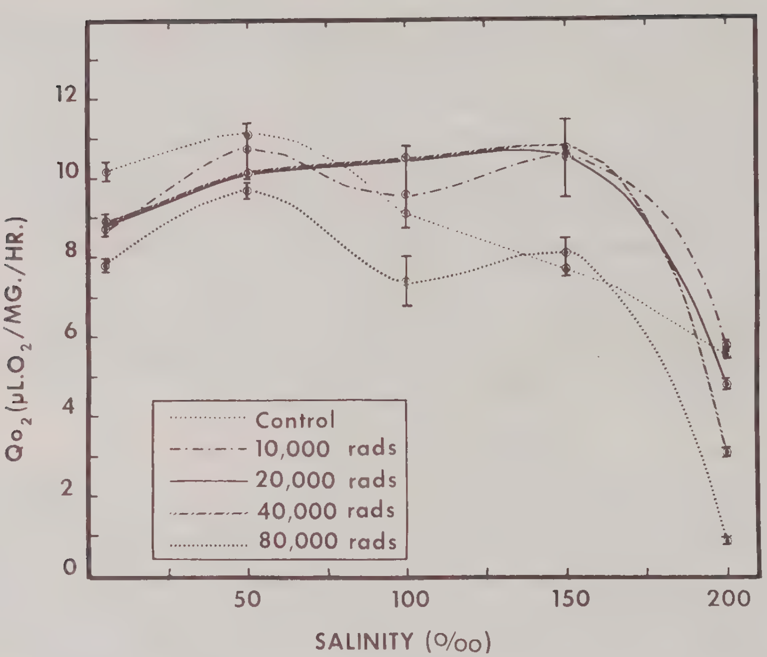

FIG. 1. Relation between the respiration rates of unirradiated and irradiated brine shrimp nauplii and the salinity of the water at 20°C. Vertical lines represent ±1 standard error for four replications.

Q_{O_2} values within the controls and within each irradiated group were higher at 50‰ salinity than at 5‰, and were lowest at 200‰, the salinity nearest that of their natural habitat. Respiration rates for the control group decreased progressively with each increase in salinity from 50 to 200‰, whereas respiration rates for each group of irradiated nauplii were nearly constant at salinities of 50 to 150‰. The apparently low Q_{O_2} for animals that received 80,000 rads and were in 100‰ salinity was not significantly different from the Q_{O_2} of nauplii that received the same dose and were in 5‰ salinity.

Analysis of variance proved that radiation and the salinity–radiation interaction also affected the respiration rates of brine shrimp. The effect of radiation was most apparent at 80,000 rads, at which dose the rate of respiration of irradiated nauplii decreased in all salinities. The effect of the interaction between salinity and radiation was also shown by the mean Q_{O_2} values. All irradiated nauplii at the lowest salinity, 5‰, and those irradiated with 40,000 or 80,000 rads in the highest salinity, 200‰, respired more slowly than the controls. Nauplii irradiated with 10,000, 20,000, or 40,000 rads in 150‰ and those irradiated with 20,000 or 40,000 rads in 100‰ respired more rapidly than the controls. Nauplii with the lowest respiration rates (those irradiated with 40,000 or 80,000 rads at 200‰) died within 24 hours after irradiation.

TABLE I

Mean Q_{10}[a] Values for Brine Shrimp Nauplii at Five Salinities and Five Radiation Doses[b]

Radiation dose (rads)	*Salinity (‰)*				
	5	*50*	*100*	*150*	*200*
0	1.98 ± .03	1.90 ± .03	1.91 ± .03	1.65 ± .04	1.73 ± .03
10,000	1.94 ± .03	1.87 ± .05	1.91 ± .03	1.81 ± .06	1.54 ± .03
20,000	1.98 ± .01	1.86 ± .02	1.84 ± .04	1.86 ± .06	1.46 ± .05
40,000	1.91 ± .03	1.89 ± .02	1.84 ± .02	1.82 ± .09	1.32 ± .01
80,000	1.94 ± .02	1.87 ± .03	2.13 ± .05	1.77 ± .06	1.43 ± .06

[a] $Q_{10} = \left(\frac{Q_{O_2} \text{ at } 30°\text{C}}{Q_{O_2} \text{ at } 20°\text{C}}\right).$

[b] Each value is the mean ±1 standard error for four replications. Q_{O_2} is known to increase linearly in this temperature range.

Effects of Radiation and Salinity on Q_{10} Values

Most of the mean Q_{10} values for unirradiated and irradiated brine shrimp nauplii for the temperature range of 20° to 30°C were near what might be expected of a thermobiologic reaction (Table I). An analysis of variance showed, however, that salinity and the salinity–radiation interaction affected the Q_{10} much more than did radiation itself. At salinities of 5, 50, or 100‰ the mean Q_{10} values for controls or any irradiated group did not differ except for the group irradiated with 80,000 rads at 100‰. This Q_{10}, larger than all others, was reproducible, but reasons for the high value are unknown. At 150‰ salinity the Q_{10} was lower for the control nauplii than for irradiated nauplii, and at 200‰ the Q_{10} for the control group was greater than for the irradiated groups. The Q_{10} values for unirradiated nauplii were similar at salinities of 5, 50, and 100‰, but decreased at 150 and 200‰. Differences were not significant among the Q_{10} values for nauplii that were irradiated with 10,000 or 20,000 rads and were in salinities of 50, 100, or 150‰. In a salinity of 5‰, however, they had a higher Q_{10}, and in a salinity of 200‰ their Q_{10} was lower. The only difference between the Q_{10} values of nauplii that were irradiated with either 40,000 or 80,000 rads (with the exception of the high Q_{10} at 80,000 rads and 100‰ salinity) was the lower Q_{10} at 200‰.

Normal Respiration Rates for Artemia Nauplii

The relation we observed between respiration rates of the unirradiated nauplii and salinity (Fig. 1) was different from those reported by Eliassen (*5*) and Kratowich (*6*). Eliassen (*5*) found that the respiration rate of brine shrimp nauplii increased as salinity decreased over a salinity range of 10 to 50‰. In the present study we noted the reverse: higher respiration rates at 50‰ than at 5‰. Kratowich (*6*) reported no difference in Q_{O_2} values of brine shrimp nauplii in salinities up to approximately 100‰. It is difficult to compare their data with ours because different methods and sometimes different strains of brine shrimp were used; however, the fact that salinity influences the metabolic rates of many aquatic organisms is well known (*7*). The effects of salinity on respiration are usually reported as increased or decreased respiration in salinities that are either subnormal or supernormal for the organism. On this basis, respiration rates that were obtained previously for brine shrimp in different salinities could not be compared with data from other animals because the "normal" respiration rate for brine shrimp had not been established under conditions approaching those of its environment. Thus, it was not possible to know whether the measured Q_{O_2} values reflected increases or decreases from normal. For our shrimp we assumed 200‰ is "normal," for they come from Great Salt Lake where the salinity varies around 220‰, and the ionic composition of the water is similar to that of the water used in the present experiment. Animals living in such an environment for generations should be genetically adapted to it. With reference to this "norm," all unirradiated animals at the lower salinities had increased rates of respiration. Increased rates of respiration in subnormal salinities have been reported previously for other crustaceans (*7*), and it has been suggested that the increased metabolic rate observed in active animals held in subnormal salinities may be due to increased random movement or to escape movements (*8*).

The Site and Nature of Radiation Damage

When the Q_{O_2}'s of the irradiated nauplii were compared as percentages of control Q_{O_2}'s, both stimulation and inhibition of respiration occurred under conditions that were identical except for salinity (Fig. 2). The respiration rates of nauplii irradiated with either 10,000, 20,000, or 40,000 rads appeared to depend more on the salinity of the water than on the amount of radiation received. Respiration of the nauplii irradiated with these doses of radiation was inhibited at 5 and 50‰ and stimulated at 100 and 150‰. At 200‰ salinity the respiration rate of the nauplii decreased with each increase in radiation dose above 10,000 rads. Investigators using other animals have observed stimulation of respiration by low doses of radiation followed by inhibition at higher levels, as we found at the higher salinities (100 and 150‰) and inhibition of respiration by all radiation doses, as in nauplii at the lower salinities—5 and 50‰ (*9, 10*).

From our data and those of others, it is possible to speculate that radiation may lessen the ability of brine shrimp to osmoregulate by inhibiting the transport of ions by the organelles in the branchiae ("gills"). The increase in respiration that we observed in irradiated nauplii at salinities of 100 and 150‰ was similar to that shown by nauplii exposed to the metabolic inhibitor 2,4-dinitrophenol (*6*). In addition to an increased rate of respiration, the internal sodium concentration of the metabolically inhibited nauplii increased at salinities approaching 100‰—the point at

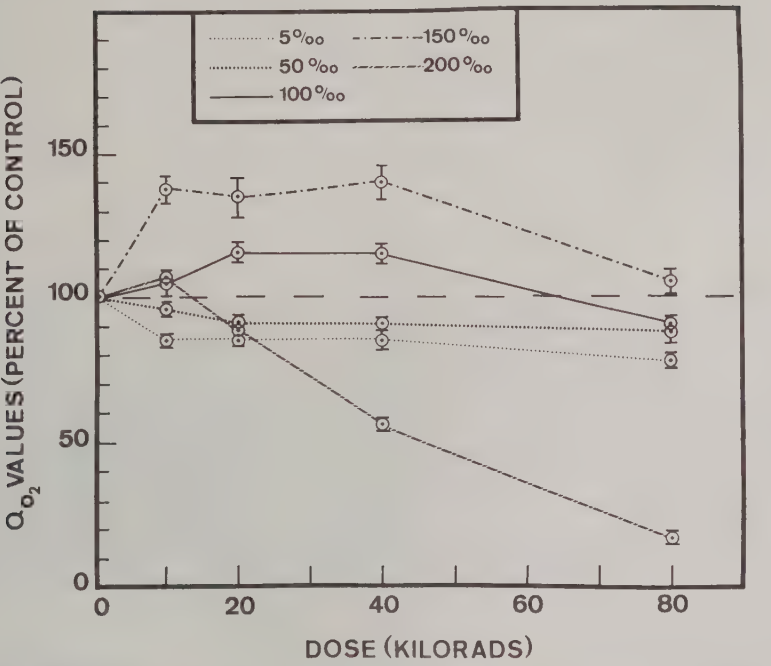

FIG. 2. Comparison of the respiration rates of irradiated brine shrimp nauplii at different salinities plotted as percentage of control respiration rates. Vertical lines represent ±1 standard error for four replications.

which we first found increased respiration in irradiated nauplii. This increase in internal sodium was attributed to decreased active transport of sodium ions outward. From the similarity between results obtained with radiation and 2,4-dinitrophenol, the assumption might be made that radiation also inhibits ion transport. If this assumption is correct, the radiation-sensitive site in the nauplii may be the metabolically active organelles in the branchiae which Copeland (*11*) suggested might be used as pumps in the metabolic transport of salt. If radiation impairs the ability of the nauplii to transport ions actively, the increased respiration rates at 150‰ salinity might reflect the additional metabolic work required for the nauplii to maintain their salt balance. The decreased respiration rates of irradiated nauplii at 200‰, however, seem to conflict with the idea that increased respiration rates reflect the inhibition of active outward transport of salt. We observed that irradiated nauplii were unable to survive in 200‰, possibly because they are unable to compensate for the inhibition caused by radiation and they succumb to the additional physiological stress imposed when they attempt to maintain their homeostasis against the greater osmotic gradient. Fish also have been found to be more susceptible to radiation at high salinities, and this sensitivity has been attributed to possible failure of their osmoregulatory system (*1*, *3*, *4*).

Brine shrimp nauplii were affected most by the interaction of radiation and salinity when they were held in salinities approaching those of their natural habitat. The highest salinity used in these experiments was well within the tolerance range of the brine shrimp and, on the basis of Grosch and Erdman's (*12*) estimates of lethal doses of radiation for adult brine shrimp (200,000 R of x-ray for males and 150,000 R for females), the nauplii also should have survived most of the radiation doses used. We found, however, that, at 200‰ salinity and after radiation doses of 20,000 rads or greater, the nauplii appeared to be under a severe physiological stress and did not survive long.

RECEIVED: October 23, 1967

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TROPICAL ATLANTIC BIOLOGICAL LABORATORY BUREAU OF COMMERCIAL FISHERIES, MIAMI, FLORIDA

TABL on Virginia Key
(Biscayne Bay), Miami, Florida

The Tropical Atlantic Biological Laboratory (TABL) of the U.S. Department of the Interior, dedicated in November of 1965 in Miami, Florida, is the latest addition to a community of Bureau of Commercial Fisheries scientific institutions dispersed throughout the country.

The plans that led to the TABL program began in 1959 when the Bureau proposed a cooperative investigation of the fishery resources off West Africa, to be performed by the U.S. and several West African states. The proposal grew into an 8-nation, 13-vessel oceanographic exploration called the International Cooperative Investigations of the Tropical Atlantic.

From the beginning, TABL's stated objectives were broad and many-faceted: the study of pelagic marine food resources of the tropical Atlantic Ocean; the design of research programs to increase the efficiency and the total catch of U.S. commercial fisheries; the acquisition of greater knowledge of surface-schooling tunas in the tropical Atlantic and adjacent seas, for use in both collecting and conserving stocks; and helping the peoples of under-developed nations bordering the tropical Atlantic Ocean (through cooperative international efforts) to find better means of using the protein-rich resources near their shores.

Oceanographic activities pursued since the creation of TABL include 12 cruises by the research vessel UNDAUNTED in nearby Florida waters, the Gulf of Mexico, the Caribbean Sea, in waters bordering South and Central America, and in the Atlantic off West Africa. Large volumes of data – oceanographic, biological, and ecological – have been gathered and assimilated. Evidence has been found that may point the way to new concentrations of tunas in the Caribbean area, and important information on the West African tuna stocks has been furnished to the U.S. tuna fleet. TABL scientists have traveled to a number of foreign countries and many U.S. regions to gather and exchange information, while the laboratory has served as host to many national and international scientific conferences. New systems involving the most modern data-processing methods have been tested and put in operation; an ichthyological reference and study collection contains more than 100,000 specimens (about 1,500 species); more than 80 scientific manuscripts have been completed; and a radio station capable of communicating with ships 6,000 or more miles away is operative.

The laboratory employs about 70 people who perform scientific, technical and clerical duties. Many of the 40-odd staff scientists and marine technicians perform dual jobs – part of their time is spent on

R/V Undaunted-TABL

Baby Billfish, captured off coast of Africa in 1968 by scientist aboard R/V Undaunted.

Senator Claiborne Pell (R.I.), May, 1968, in lobby of TABL, before a fossil display

scientific studies ashore and part aboard the UNDAUNTED. Sometimes twice in 1968 for instance – this schedule can mean a 5- or 6-month tour of duty in developing countries in the eastern tropical Atlantic.

At present, most TABL investigations and surveys concentrate on the six species of tuna found in the tropical Atlantic. Everything about these fish is under examination – their life cycles, migratory routes, feeding habits, breeding patterns, genetics, seasonal changes, and fluctuations in abundance. To a lesser degree, tuna forage fishes are under study. Research must take into account the effects of weather, tides, and currents on different species; the nutrient content, chemical composition, and temperatures of seawater; availability of smaller food fish; chances for survival of larval and juvenile tunas in different areas under a variety of circumstances; and oceanographic measurements of currents and other marine features. All these data must be converted into forms that lend themselves to computer analysis.

To carry out the central responsibility of the Bureau of Commercial Fisheries – to assist and improve commercial fisheries in the U.S. – continual attention must also be devoted to searching out practical methods of conserving stocks while simultaneously increasing the total U.S. catch.

RESEARCH PROGRAMS

The TABL organization is divided, roughly, into six dovetailing functions:

1. **Tuna Fishery Biology Program.** Strives to reach an understanding of the ecology and relation to the environment of the tropical Atlantic tuna stocks. Inherent in this understanding is the determination of optimum equilibrium yield for efficient fishing.
2. **Developmental Biology of Tunas Program.** Investigates the biology of eggs, larvae and juvenile tunas, with particular attention to distribution, growth, and mortality.
3. **Fishery Oceanography Program.** Studies the physical, chemical, and biological environment in which all links in the oceanic food chain operate, and how this environment affects the separate elements in the chain.
4. **Systematics Program.** Identifies and studies fishes and their evolution, particularly species from the western and tropical Atlantic Ocean. Curates the ichthyological collection.
5. **Calico Scallop Biology Program.** Studies and determines significant biological characteristics of scallop stocks as an aid to the estimation of sustainable levels of exploitation.
6. **Technical Services/Marine Service/Administrative Services.** The three units provide support for the five research programs. Among their duties are chemical analyses, data processing, and operation of the vessel and the 1,000-watt, 4-frequency radio station (KAG).

PHYSICAL DESCRIPTION OF THE LABORATORY

Many sites were considered before TABL was built, but Miami was chosen because it offered an impressive list of advantages, including the opportunity for mutually beneficial associations with the nearby Institute of Marine Sciences of the University of Miami, the planned ESSA laboratory, and the Miami Seaquarium. Director Carl J. Sindermann points out that the location of the laboratory makes it an almost perfect base from which to pursue many oceanographic objectives – the Florida Current portion of the Gulf Stream, with its almost boundless opportunities for oceanic research, passes almost within sight of shore; small craft and research vessels can easily reach the scientifically interesting Bahamas Banks, the Gulf of Mexico, and many Caribbean areas; southeast Florida is admirably situated as a base for deep-sea studies in the regions between it and West Africa, South America, the Caribbean, and Bermuda; and nearby waters teem with a large quantity and variety of marine life.

"TABL's setting offers another intangible but highly important benefit – the opportunity to be part of an almost unique fishery-oceanography community," Dr. Sindermann said. "Virginia Key, though only minutes from downtown Miami, has none of the complexities and distractions of urban surroundings. Construction on the island is limited almost entirely to fishery-oceanography establishments, all built near each other and fronting on Biscayne Bay and the Atlantic. The special ambience of the island is unusually suited to the work of marine scientists."

The air-conditioned laboratory, which stands on 5 acres of land, is a three-story, two-wing structure made of precast, prestressed concrete, and contains 48,300 square feet of covered space. In addition to the usual accoutrements of a biological laboratory, TABL houses a large aquarium room with specially designed fish tanks and an electrically operated ceiling monorail for the transfer of heavy specimens to tanks. A controlled environment room is partitioned with a two-way mirror so that young fish can be studied without disturbing normal behavior. Each of the 12 individual laboratories has outlets for compressed air, gas, hot and cold running freshwater, and running seawater. A building at the rear of the laboratory contains two 30,000-gallon settling tanks for the seawater system. Seawater (500 gallons per minute) is piped into the laboratory from a submerged intake crib in nearby Bear Cut through a dual pipe system made of non-toxic material. A diesel-powered emergency generator ensures that power will not be interrupted.

Originally commissioned in 1944 as an ATA-class (seagoing) Navy tug, the UNDAUNTED was converted into a Bureau research vessel in 1965. She is 143 feet long with a 34-foot beam and 12-foot draft; speed is 10 to 12 knots and cruising range is about 5,000 miles. The ship is equipped for live-bait fishing and for either benthic or pelagic trawling, as well as for oceanographic observations at varying depths. She carries a salinity-temperature-depth (STD) system for measuring characteristics of seawater, a 25-channel data acquisition system, and an automatic picture-transmission receiver for working in conjunction with NASA satellites on broad-scale oceanography. Also aboard the vessel are: laboratories for chemical analysis and general biology; electronic equipment; a live-bait tank holds 2,000 pounds of fish; and two single side-band radio transmitters for voice contact with the home laboratory's radio station and for rapid transmission of data from ship to shore. Quarters include six staterooms for scientists and nine cabins for crew members, which accommodate a total of 25 people.

By the end of 1968, the UNDAUNTED will have participated in 12 research voyages through tropical Atlantic waters. During her tenure with TABL, the vessel has logged some 700 days at sea, steamed about 100,000 miles, and collected many thousands of samples of marine fauna. She has touched port in Bermuda and the Bahamas, in many Caribbean islands, and in South America and Africa.

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Comparison of Meristic Characters of Adult Atlantic Herring from the Gulf of Maine and Adjacent Waters

BY VAUGHN C. ANTHONY[1] AND H. C. BOYAR[1]

Abstract

Counts of vertebrae and of rays of the right pectoral, dorsal, and anal fins were examined from 5,829 Atlantic herring of the 1958 and 1960 year-classes collected in 1962–65 from areas of Cape Cod, Western Maine, Eastern Maine, Southern Nova Scotia, and Georges Bank. Meristic counts were not significantly different between sexes. Differences in meristic counts among years of sampling were significant, indicating a change in the distribution of herring for a particular year for a given area. Counts of vertebrae and rays of the right pectoral fin suggested that two complexes of herring existed: a Georges Bank-Cape Cod complex which was significantly different from a Maine-Nova Scotia complex. The magnitude of differences among areas in the mean meristic counts for herring of the 1958 year-class was greater than for fish of the 1960 year-class.

Introduction

The racial differences of stocks of Atlantic herring, *Clupea harengus harengus* L., in the Gulf of Maine are being studied by the U. S. Bureau of Commercial Fisheries at the Boothbay Harbor Biological Laboratory. Serological methods; age, length, and maturity data; parameters of growth; and meristic characters are being investigated as indicators of racial differences. This paper gives the results of the investigation of meristic characters of adult herring in the Gulf of Maine and adjacent waters.

Rounsefell and Dahlgren, 1932; Tester, 1937; McHugh, 1942; Bückmann, 1950; and others have found that counts of vertebrae and fin rays of herring increase with a latitudinal decrease in temperature. If this increase holds for herring in the Gulf of Maine and adjacent waters and if herring remain in or return to their respective areas of birth, they should exhibit meristic counts typical of that environment; in particular, counts should be higher in colder waters.

The time in the ontogeny of Atlantic herring when the counts of vertebrae and fin rays are fixed is not known. Tåning's (1952) work with brown trout, *Salmo trutta trutta* L., indicates that the number of vertebrae is determined before hatching, and that the period of fixation for the anal fin begins in the egg stage but continues after hatching. The dorsal and then the pectoral fins are formed next. Gabriel (1944) showed for *Fundulus heteroclitus* (L.) and Dannevig (1950) for *Pleuronectes platessa* (L.) that the number of vertebrae is determined during incubation of the egg. Hempel and Blaxter (1961) reported that the myotome count of Atlantic herring is determined before hatching, although Bückmann (1950) and Tester (1938) gave evidence that the number of vertebrae is at least partially determined after the eggs have hatched. Bigelow and Schroeder (1953) gave 15–17 mm and Blaxter (1962) gave 13–14 mm as the lengths at which the dorsal fin is formed.

Atlantic herring spawn in the Gulf of Maine from late August through October. The eggs are demersal and incubate 10–15 days before hatching, after which the larvae rise to the surface waters. If the meristic characters are fixed while the herring are in this larval stage, the temperature of the surface water would influence development.

Collection and examination of samples

Adult herring were sampled in the Gulf of Maine and adjacent waters in 1962–65. Coastal samples (mostly from spawning schools) were obtained from Stonington, Connecticut, to Grand Manan, New Brunswick, and from St. Mary's Bay to Port Mouton, Nova Scotia; offshore samples were from Georges Bank. Counts of fin rays (right pectoral, dorsal and anal) and vertebrae were made for 100 fish from each collection with the aid of a low power (10× to 30×) dissecting microscope. Vertebral counts excluded the hypural plate. The 1958 and 1960 year-classes of herring—the two dominant year-classes from 1962 to 1967—were chosen for analysis (Table 1). Since

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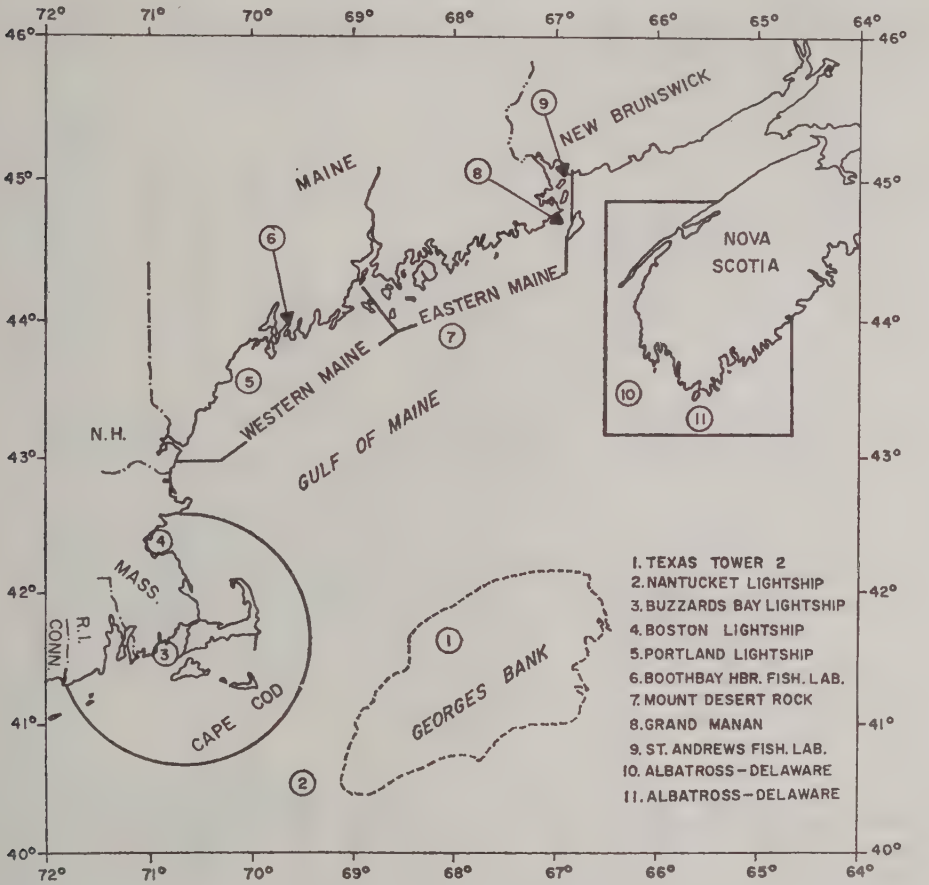
TABLE 1. Mean counts of vertebrae and of fin rays in the right pectoral, dorsal, and anal fins of the 1958 and 1960 year-classes of Atlantic herring, by years and areas of sampling, and probabilities that the mean counts are not different among years.

Area and Year	Number of fish		Vertebrae		Right pectoral fin		Dorsal fin		Anal fin	
Year-class:	1958	1960	1958	1960	1958	1960	1958	1960	1958	1960
Nova Scotia										
1962	53	—	55.5283	—	18.4717	—	19.3774	—	17.9434	—
1963	283	133	55.5830	55.4060	18.4806	18.2632	19.3145	19.4587	17.9152	18.1579
1964	129	291	55.4729	55.4914	18.5039	18.3849	19.3876	19.4399	18.1240	18.1615
1965	185	540	55.5730	55.5519	18.4108	18.4963	19.5514	19.4944	18.1405	18.1815
1962–65	650	964	55.5538	55.5135	18.4646	18.4305	19.4015	19.4730	18.0231	18.1722
Probabilities			P > .25	P < .10	P > .25	P < .01	P < .01	P > .25	.01 < P < .05	P > .25
Eastern Maine										
1963	97	—	55.6495	—	18.5361	—	19.5567	—	18.2062	—
1964	38	185	55.3421	55.4973	18.2895	18.4000	19.5000	19.4324	18.2105	18.2324
1965	31	641	55.3871	55.4774	18.6775	18.4571	19.4194	19.4415	18.2258	18.1061
1963–65	166	826	55.5301	55.4818	18.5060	18.4443	19.5181	19.4395	18.2108	18.1998
Probabilities			.01 < P < .05	P > .25	P < .25	P > .25	P > .25	P > .25	P > .25	P > .25
Western Maine										
1963	211	233	55.5924	55.4764	18.4265	18.2146	19.5356	19.4741	18.0237	17.9399
1964	82	315	55.3781	55.4064	18.3537	18.3302	19.3293	19.2857	18.0976	18.1016
1965	111	401	55.5496	55.4763	18.3784	18.3990	19.5676	19.5162	18.1712	18.1671
1963–65	404	949	55.5371	55.4531	18.3985	18.3309	19.5025	19.4215	18.0792	18.0896
Probabilities			.01 < P < .05	P > .25	P > .25	.01 < P < .05	.01 < P < .05	P < .01	P > .25	P < .01
Georges Bank										
1962	261	—	55.4061	—	18.1648	—	19.1916	—	18.0575	—
1963	265	389	55.2793	55.3342	18.0340	18.0257	19.3849	19.4396	18.0906	18.0540
1964	157	834	55.3440	55.4089	18.1783	18.2062	19.2994	19.4353	18.0892	18.1391
1965	51	632	55.1765	55.3354	18.1765	18.1013	19.4118	19.4035	18.2157	18.1155
1962–65	734	1855	55.3311	55.3682	18.1213	18.1326	19.2998	19.4253	18.0872	18.1132
Probabilities			P < .25	P < .10	P < .25	P < .01	P < .01	P > .25	P > .25	P > .25
Cape Cod										
1963	169	—	55.3550	—	18.1420	—	19.3195	—	17.9882	—
1964	152	296	55.2303	55.3311	18.0395	18.1892	19.2895	19.4493	18.1184	18.1926
1965	—	361	—	55.3490	—	18.2133	—	19.3989	—	18.1607
1963–65	321	657	55.2960	55.3409	18.0935	18.2024	19.3053	19.4216	18.0498	18.1750
Probabilities			P < .25	P > .25	P < .25	P > .25	P > .25	P > .25	P < .25	P > .25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EASTERN MAINE
WESTERN MAINE
GULF OF MAINE
N.H.
MASS.
R.I.
CONN.
CAPE COD
GEORGES BANK
1. TEXAS TOWER 2
2. NANTUCKET LIGHTSHIP
3. BUZZARDS BAY LIGHTSHIP
4. BOSTON LIGHTSHIP
5. PORTLAND LIGHTSHIP
6. BOOTHBAY HBR. FISH. LAB.
7. MOUNT DESERT ROCK
8. GRAND MANAN
9. ST. ANDREWS FISH. LAB.
10. ALBATROSS – DELAWARE
11. ALBATROSS – DELAWARE
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Fig. 1. Gulf of Maine, showing areas of investigation and locations (encircled numbers) where temperature data were collected.

little was known about the identity and boundaries of stocks within the Gulf of Maine, five arbitrary areas were selected: Western and Eastern Maine, Nova Scotia, Georges Bank, and Cape Cod (Fig. 1).

Since the time of fixation of meristic characters is not precisely known, and since bottom temperatures at the spawning sites are unavailable, the mean temperatures of surface water for September–October were used for comparisons among areas (Table 2 and Fig. 1). The differences in surface temperature were pronounced; temperatures were lowest in the Nova Scotia and Eastern Maine areas, and were lower in 1958 than 1960 in all areas.

Methods of analysis

We examined the differences of the meristic characters between years of sampling and between sexes for each of the two year-classes to see if the data for different years of sampling and for both sexes could be combined. Because sample size varied among years and areas, unequal variances would invalidate analysis of variance procedures and comparisons based on the *t*-distribution. The Bartlett test (Brownlee, 1960) was therefore used to test for homogeneity of variance for meristic data sampled among years, for each sex, area, and meristic character. Six of eighty comparisons were significantly different ($P \leq 0.05$) instead of the expected four at the 5% level which indicates

TABLE 2. Mean temperature (°C) of surface waters in September–October, 1958 and 1960, at selected sites in the Gulf of Maine and adjacent waters.

Area, station number, and site[a]	Year 1958	Year 1960
Georges Bank:		
1. Texas Tower 2	14.8	15.5
Nantucket Shoals:		
2. Texas Tower 3	—	15.5
Cape Cod:		
3. Buzzards Bay Lightship	15.9	16.6
4. Boston Lightship	12.8	14.3
Western Maine:		
5. Portland Lightship	11.8	12.6
6. Biological Laboratory, Boothbay Harbor	11.9	12.3
Eastern Maine:		
7. Mount Desert Rock	—	10.8
8. Grand Manan Island	11.4	—
9. Biological Station, St. Andrews, N. B.	11.5	11.7
Nova Scotia:		
Albatross-Delaware cruise	10.2	—
Albatross-Delaware cruise	12.5	—

[a]See Fig. 1 for locations of stations.

that, generally, the variances are not different among years. Bartlett's test, however, is sensitive to nonnormality and may falsely reject the hypothesis of equality of variance when the frequency distribution is heavily concentrated about the mean (Scheffé, 1959), (as it is for vertebral counts of herring). Because three of the six significant values were with vertebral data and may have been partially due to nonnormality, the assumption of homogeneity of variances is strengthened. The inferences associated with the *t*- and the *F*-distributions also are not seriously affected by nonnormality.

Two-way analysis of variance tests were conducted between years of sampling and sexes. The probabilities that the mean counts are not different among years are entered in Table 1. There were no significant differences in meristic counts between sexes. Some mean meristic counts, however, were significantly different from year to year for a given year-class within an area. Each area may have contained several stocks of herring, but more likely the herring in the Gulf of Maine and adjacent waters were not distributed similarly in successive years. For example, on Georges Bank in June, 1964, the herring of the 1960 year-class had a significantly higher ($P \leq 0.05$) meristic count than all other herring obtained from Georges Bank; in the fall, this difference no longer existed. If the generalization is true that higher meristic counts exist in herring from colder water, then herring of this type apparently moved onto Georges Bank in June, and were replaced with a different group in the fall.

In 1965 samples of both the 1958 and 1960 year-classes of herring from southern Nova Scotia also had unusually high meristic counts (Table 1). The counts of the rays of the right pectoral fin for the 1960 year-class and the counts of the rays of the dorsal fin for the 1958 year-class were significantly higher ($P \leq 0.01$) in 1965 than samples collected in other years. The *t*-test, adjusted for planned comparisons, was used to determine the year or years responsible for the significant differences. This test consists of allocating beforehand the chosen total error probability α (in our

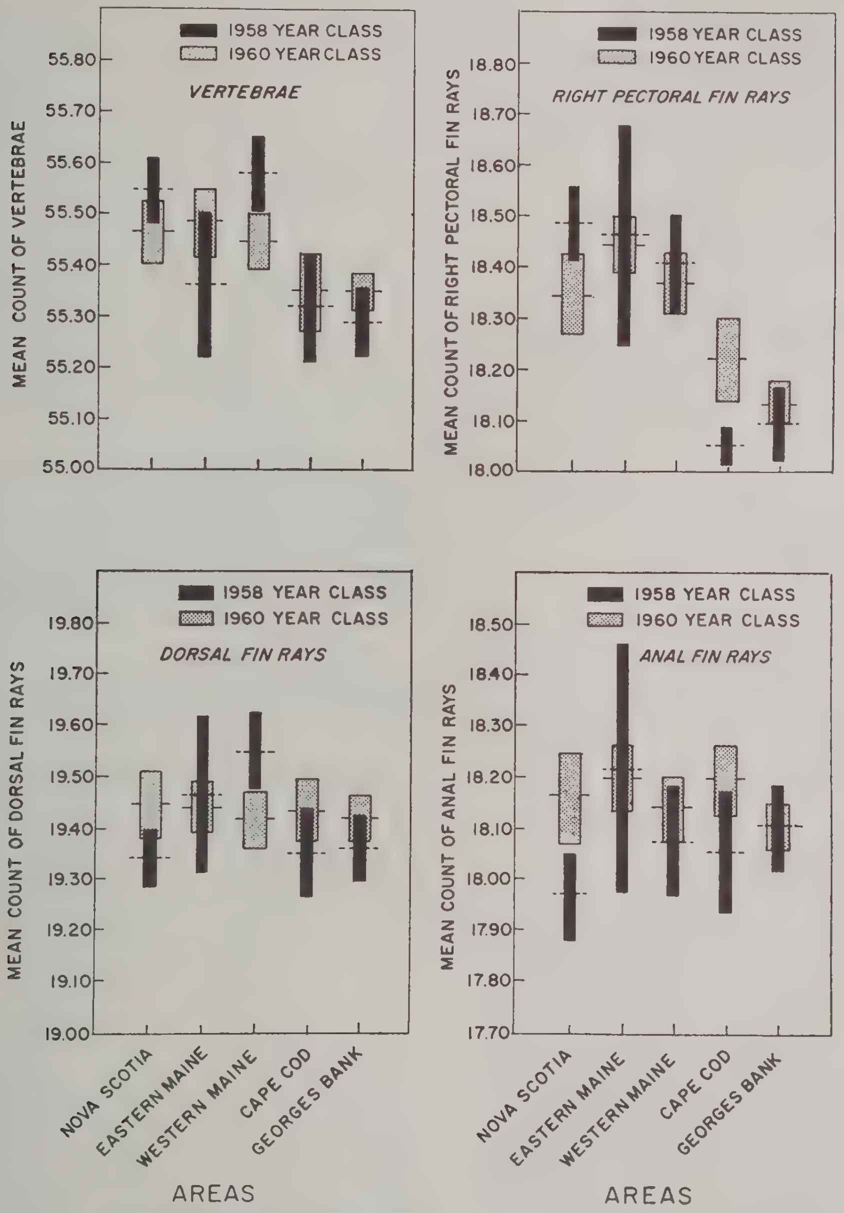

Fig. 2. Mean counts of four meristic characters by area and year class (horizontal lines indicate means; vertical bars indicate two standard errors on each side of the mean).

case = 0.05) into components $\{\alpha_1^*, \ldots, \alpha_m^*\}$ for the m comparisons of means to be covered by the *t* confidence intervals so that $\sum_{i=1}^{m} \alpha_i^* = \alpha$. The confidence interval about the difference between means is

$$\bar{x}_i - \bar{x}_j \pm t_{\alpha^*} \sqrt{S^2\left(\frac{1}{n_i} + \frac{1}{n_j}\right)}$$

where S^2 is the error mean square from the one-way analysis of variance. The probability that all of these intervals simultaneously cover the true values is then $\geq 1 - \sum_{i=1}^{m} \alpha_i^*$ (Scheffe, 1959) and the adjusted *t*-test is then

$$t_{\alpha^*} = \frac{\bar{x}_i - \bar{x}_j}{\sqrt{S^2\left(\frac{1}{n_i} + \frac{1}{n_j}\right)}}$$

This is a planned comparison technique and avoids the wide intervals encountered with unplanned comparison techniques. When used to test for differences between means, the null hypothesis tends to be rejected more easily than with an unplanned comparison technique.

In Western Maine, meristic counts were significantly different between years for five of eight combinations of meristic characters and year-classes. For the 1958 year-class, vertebral and dorsal ray counts were significantly lower in 1965 than in other years; for the 1960 year-class, right pectoral and anal ray counts were significantly lower in 1963 and dorsal fin ray counts in 1964.

Samples of herring were discarded from further analysis when they were significantly different ($P \leq 0.05$) from all other samples collected within the same area and when the differences were present in several meristic characters, because we assumed that the discarded herring belonged to groups or stocks not normally found in that area.

Fish excluded from the samples of Nova Scotia and Eastern Maine had unusually high meristic counts and those discarded from Georges Bank (other than the samples of the 1960 year-class collected in June, 1964) and Western Maine, had unusually low meristic counts. Such discarding of data does not create significant differences between areas but reduces the probability of herring from two areas having significantly different meristic counts, because the counts of fish from Nova Scotia and Eastern Maine are generally much higher than those from Georges Bank and Cape Cod and about the same as those from Western Maine. The single possible exception is Western-Eastern Maine; the counts of the right pectoral rays for the 1960 year-class might have indicated that herring from Eastern Maine were significantly different from herring of Western Maine if all available data from Western Maine had been used. The remaining data were combined for different years of sampling and for both sexes. The area means and their reliability are shown in Fig. 2.

The combined data for each year-class and meristic character were tested for differences among areas by a one-way analysis of variance test and by adjusted *t*-tests to determine the significance of each area comparison (Table 3). The assumptions of normality and equality of variance required for variance analysis were satisfied.

The probabilities (P_i) that two areas do not differ were combined for the four meristic characters for each year-class according to Fisher (1963) where $-2 \sum \log_e P_i$ is distributed as chi-square with twice as many degrees of freedom as there are P_i to be combined. Disadvantages of combining in this fashion are that all four meristic counts are treated equally and each P_i is treated as being independent. No conclusions are possible from the dorsal and anal fin ray data by themselves, but the counts of vertebrae and right pectoral fin rays show similar and distinct differences.

Comparison of Areas

Adult herring from Georges Bank and Cape Cod have similar meristic counts, as, in general, do herring from Eastern Maine, Western Maine and Nova Scotia. Some differences in meristic counts between Nova Scotia and Western Maine, however, are not clearly explainable. The counts of the right pectoral fin rays of the 1958 year-class were significantly lower in Western Maine than in Nova Scotia, and the counts of the dorsal fin rays of the 1958 year-class were significantly higher (Fig. 2). On the basis of an adjusted *t*-test, the general significance level between Nova Scotia and Western Maine is $0.05 > P > 0.02$. A one-way test between these two areas would not indicate

TABLE 3. Probabilities based on four meristic characters that herring from two areas do not differ.

Area comparisons by year-class	Vertebrae	Right pectoral fin	Dorsal fin	Anal fin	Total for each year-class
Nova Scotia vs. Georges Bank:					
1958	<.005	<.005	>.900	.230	<.005
1960	.030	<.005	>.900	>.900	<.005
Western Maine vs. Georges Bank:					
1958	<.005	<.005	<.005	>.900	<.005
1960	.030	<.005	>.900	>.900	<.005
Western Maine vs. Cape Cod:					
1958	<.005	<.005	<.005	>.900	<.005
1960	>.900	<.005	>.900	>.900	<.250
Nova Scotia vs. Cape Cod:					
1958	<.005	<.005	>.900	>.900	<.005
1960	.040	.030	>.900	>.900	>.500
Eastern Maine vs. Georges Bank:					
1958	>.900	<.005	>.900	>.900	<.005
1960	<.005	<.005	>.900	.100	<.005
Eastern Maine vs. Cape Cod:					
1958	>.900	<.005	.697	>.900	<.005
1960	<.005	<.005	>.900	<.900	<.005
Nova Scotia vs. Western Maine:					
1958	>.900	<.005	<.005	>.900	<.005
1960	>.900	>.900	>.900	>.900	>.900
Cape Cod vs. Georges Bank:					
1958	>.900	>.900	>.900	>.900	>.900
1960	>.900	<.005	>.900	.700	<.025
Eastern Maine vs. Western Maine:					
1958	.180	.300	>.900	>.900	>.900
1960	>.900	.290	>.900	>.900	>.900
Nova Scotia vs. Eastern Maine:					
1958	.350	>.900	>.900	.343	>.900
1960	>.900	.370	>.900	>.900	>.900

that the fish from Nova Scotia had overall significantly higher counts. A one-way test, however, assumes that meristic counts increase with a decrease in water temperature, which we are investigating here and cannot assume at this point. This variability of meristic data in Western Maine suggests that stocks frequently intermingle there.

The mean counts of vertebrae and right pectoral rays for the 1958 and 1960 year-classes were significantly different ($P \leq 0.05$) between Nova Scotia and both Georges Bank and Cape Cod, and between Western Maine and Georges Bank. Evidence that herring from Western Maine and Cape Cod are different is given by the mean counts of the rays of the right pectoral fin for both year-classes and the vertebral counts for the 1958 year-class ($P \leq 0.005$). The vertebral counts for the 1960 year-class and the counts of the right pectoral fin rays for both year-classes indicate that Eastern Maine is also significantly different ($P \leq 0.005$) from both Georges Bank and Cape Cod. These differences combined with the similarities between both sections of Maine and Nova Scotia and between Cape Cod and Georges Bank, suggest that herring from Coastal Maine and Nova Scotia form one complex of herring which are significantly different from a Georges Bank-Cape Cod complex.

Comparison of year-classes

Although both year-classes generally indicated the same areal differences, the meristic counts were not similar between the two year-classes in their magnitude or in relation to temperature. The magnitude of differences in the mean meristic counts among areas for fish of the 1960 year-class was less than for fish of the 1958 year-class. Herring of the 1960 year-class from Nova Scotia and Maine, for example, were very similar in all meristic characters, indicating that fish may have mixed between the two areas.

The mean counts of the 1958 year-class for the areas of Maine and Nova Scotia were greater than those of the 1960 year-class, as we had expected from the water temperatures (Fig. 1). The mean counts of the 1958 year-class for the areas of Georges Bank and Cape Cod, however, were consistently less than those of the 1960 year-class, even though the water temperatures were lower in 1958 than in 1960, which may have been due to a variation in spawning time from year to year irrespective of temperature.

Conclusion

Despite the year-class differences, the two year-classes independently indicate consistent areal differences for a given meristic character and provide evidence of the existence of two general groups of herring within the Gulf of Maine. The composition of each complex is not yet known and more than one stock may, in fact, exist within a complex. Indeed, the herring discarded because of high or low meristic counts were assumed to come from other groups within or on the periphery of the Gulf of Maine. The herring discarded from northern waters were those with high counts indicating that they belonged to more northern, colder waters, and those discarded from the southern waters were those with low counts indicating that they belonged to more southern, warmer waters. The present data, however, show clearly that two complexes of herring exist within the Gulf of Maine and that if sub-groups are present within each complex, they are much more nearly alike than are the two complexes.

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SPACE PHOTOGRAPHY OF SOME OCEANIC PHENOMENA AND COASTAL PROCESSES

James S. Bailey and Robert E. Stevenson

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SPACE PHOTOGRAPHY OF SOME OCEANIC PHENOMENA AND COASTAL PROCESSES[1]

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Introduction

The world ocean is a dynamic system covering 71 percent of the earth's surface. The lack of synoptic data from the world ocean limits the oceanographer in understanding the processes producing many observable oceanic phenomena. Most of the existing explanations of oceanic features are conjectural because of the limited number of observations made using conventional techniques. Such observations are not proving fruitful in the development of new knowledge of the interrelationships of the ocean-atmosphere-land system.

The inadequacy of current synoptic data-gathering systems becomes apparent when viewed from the standpoint of time. The unique advantage of the satellite for oceanic studies is the capability of real-time synoptic coverage of the earth's surface. Furthermore, the coverage is rapid and repetitive, thus eliminating the major constraints to the measurement of oceanic phenomena; i.e., the vastness and remoteness of the world ocean and its time variant features. The fundamental problem today is how to acquire truly synoptic data in a usable, valid, and operational time frame. The problem can now be solved by the "view-from-space," for all major oceanographic phenomena can be measured by one or more of a combination of "on-the-shelf" remote sensors.

Coastal Processes in the Laguna de Terminos (Figure 1)

Laguna de Terminos is approximately 42 statute miles in length and 18 statute miles wide. The Laguna and surrounding land comprise about 3,300 square miles in the field of view of this photograph.

The direct utility of space photography to the study of coastal oceanographic phenomena is apparent from this photograph. The photographic situation is quite optimal here in that the Gulf water is clear and calm, and the colloidally suspended and current rafted material is light in color. Under these conditions of contrast, several active coastal processes are readily viewed at one instant in time.

Laguna de Terminos is a topographically low indentation in the Yucatan Peninsula. A series of small, fringing marshes and lagoons are evident around the major lagoon. These areas are slowly being filled with sediment from the three river systems evident on the photograph. The mud flats and associated brackish-water bodies support a mangrove type of vegetation.

This photograph was taken in August 1965, when the region was experiencing a period of maximum rainfall. Large quantities of detrital and colloidal suspended material were being discharged into the ponds and lagoons as well as Laguna de Terminos. The low relief of the Yucatan Peninsula and the soluble surface material extant preclude the accumulation of any sizable quantity of sand. The Laguna was, therefore, slowly filling with a light-colored, calcareous mud with intermixed silty and fine sand material. Most of this material can only be deposited in the Laguna during the period of intermediate to low tide when the fringing ponds and lagoons can empty into the Laguna. This process can be seen in action on the photograph. Note the two discharge channels from Rio Palizada (southwest) through which material was flowing at that instant. This easily detected pattern is one means of determining the direction of flow of the water.

Movement of water leaving the Laguna creates a turbulence which induces a scouring action on the Laguna bottom and in the inlet channel, and disperses the colloidal particles into the offshore waters. The eastern channel is the primary inlet for the flood waters, noted by the buildup of deltaic bars. Most of the Laguna discharge flows through the western channel. As a consequence, less turbulence occurs in the eastern portion of the Laguna, and the fresh water entering from the Rio Pargos is evident in this area.

[1] Contribution No. 264, Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas.

The most obvious action depicted on the photograph is the discharge of water and sediment through the western channel. The tidal velocity at this time was not of sufficient magnitude to overcome effects of the westerly longshore current. Tide tables show that at the time of the photograph (1409 hours) the tide was ebbing from a high of 2.7 feet at 0214 hours to a low of 0.6 feet at 1637 hours. Tonal variation in the photograph makes it quite easy to follow the sequence of events during this tidal recession.

The westerly longshore current was transporting sediments to the west while some of the colloidal material was carried farther out in the Gulf where it was less effected. An interesting countercurrent, or eddy, developed above the left end of Isla del Carmen.

Sandbar development can easily be seen along the coast to the right of the east channel. These bars are developed and oriented by incoming waves and longshore currents reacting on the silts and sands forming the Gulf floor at this locality. This detrital material is being transported to the west. Sandbar migration is one type of sedimentary transport induced by current and wave action. These bars have developed in water about 12 feet deep.

The coastal area between Rio de San Pedro and San Pablo, the western channel, and the central portion of the Isla del Carmen distinctly shows the structural remnants of high water and wind action. These structural lineaments paralleling the coast are sand ridges (beach ridges) with intervening troughs containing sufficient soil to support assorted vegetation including palm trees.

Texas & Louisiana Currents & Coastal Processes
(Figure 2)

The Texas and Louisiana Gulf coast is a particularly shallow shelf region with the water attaining 300 feet in depth as far offshore as 80 nautical miles.

Water-mass buildup in the Texas Gulf region is related in part to the duration and force of the prevailing southeasterly and sporadic northeasterly winds.

This photograph depicts conditions existing in the region 2 days after the passing of a cold front with the winds continuing to blow out of the northeast at 10-15 knots.

Winds accompanying the passing cold front provide sufficient force to partially drain the estuaries and lagoons within the region. Such action is shown by the light brown, sediment-laden waters being driven out of Sabine Lake and Galveston Bay. Sediments are being transported southwest along the coast by the wind-induced longshore current.

Lighter colored colloidal material has been carried further offshore by the relatively turbulent water of the Gulf and the several frictional eddies extending along the shallow shelf. The large eddylike structures are major oceanic features and are similar to rip currents in that they are "relief currents" of water piled up against the shore of the northwest Gulf.

The significance of being able to photograph repeatedly coastal waters is clear. This is especially so in these waters in which lie the greatest shrimp fishery in the world. Two key events in the lives of these shrimp are their migration to the coastal estuaries as postlarvae, and from the estuaries as juveniles and adults.

An analysis was made of the amounts and locations of shrimp caught during this period in November. This study revealed that the shrimp were caught directly beneath, or within, the major eddylike, or rip-current features. Additionally, a few shrimp were caught in the lee of the interference eddy immediately west of the Galveston jetties.

It is significant then, to be cognizant of all current systems within an area at all times to adequately predict the potential locations of various fisheries.

Quite clearly, the recognition and monitoring of such large-scale features can only be derived from recordings of the great overview unique to orbiting vehicles.

Upwelling and Taiwan
(Figure 3)

The major current system in the western Pacific Ocean flows from south to north past the island of Taiwan. Around the island, and especially in the Formosa Straits, the currents are complicated by the tides which ebb to the south along the southwestern shores of Taiwan.

On July 19, the day before this photograph was taken, tropical storm "Nina" was about 90 nautical miles east of Taiwan. The storm was not well developed and winds of Beaufort Force 3 were the highest recorded. By 1200 hours

(GCT), July 20, the storm had dissipated and winds of Force 2 blew around Taiwan from an easterly direction.

In the photograph, the light blue of the sea is the result of a diffuse sun's reflection from an evenly roughened sea surface. Winds from the east and northeast increased the roughness of the northerly flowing waters. The reflective, specular pattern from the sea surface thus depicts the features of water motion around the southern end of Taiwan.

The major current is parted by the island much as a ship parts the water. As the "bow" wave spreads from the island, upwelling must take place near the shore. The dark blue water masses east and west of the island represent the areas of major upwelling.

Areas of upwelling are known to provide nutrient waters for some fisheries. The fishing ports along the west coast of Taiwan are concentrated north of the lagoonal complex on the southwest coast. Quite possibly this photograph shows for the first time that phenomena which may be responsible for the support of the Taiwan fisheries.

A detailed oceanographic survey of the southwest coast shown here should provide conclusive data as to the relation of the upwelling area and the Taiwan fisheries.

Robert E. Stevenson received his bachelor degree from UCLA in 1946, masters from UCLA in 1948 and doctorate from the University of Southern California in 1954. From 1953 to 1961 he was the Director for Inshore Research at the Allan Hancock Foundation, University of Southern California. In 1961 he came to Texas as research scientist in the Department of Oceanography and Meteorology at Texas A & M University and in 1962 became Director of the A & M Marine Laboratory in Galveston. In 1963 he joined the staff at Florida State University as research associate in the Oceanographic Institute, Associate Professor in the Department of Geology, and Associate Professor in the Department of Meteorology. He then left Florida in 1965 to accept a position at the Bureau of Commercial Fisheries in Galveston where he is now the Assistant Laboratory Director.

Convergence Phenomena
Florida, Cuba, and Bahamas
(Figure 4)

The spacecraft doors were open and Lt. Col. Aldrin was standing on the cockpit seat as he photographed southern Florida, the western portion of the Bahama Banks, Cuba, Yucatan (on the horizon), and portions of the Caribbean Sea and the Gulf of Mexico.

Sun angle is a very significant factor in the sensing of oceanic phenomena. In this photograph the glitter pattern of the sun's reflection enhances the surface expression of an area of divergence paralleling the west coast of Florida. The diffuse reflection is a result of a roughened water surface while the elongated darker blue area of convergence represents a smoother water surface.

The existence of the divergence feature seen here has been suspected for some time and has been examined in part by oceanographers using standard oceanographic survey methods. The great size, configuration, and accurate positioning of such a feature can only be recognized and accomplished by using the overview provided by the spacecraft and the recognition and data gathering by a trained observer. A convergent feature such as this is most significant to commercial fisheries throughout the world ocean. Such conditions are particularly significant within the north and south 40° latitudes.

James S. Bailey received his PhD degree in Engineering Geology from the University of Arizona in 1955. Since that time he has conducted research for a major oil company and recently served as geological oceanographer for the NASA/Navy, Space Oceanography Project. He is now with the Bureau of Commercial Fisheries in Galveston, Texas, and is project leader for the Space Applications to Fisheries Oceanography Project.

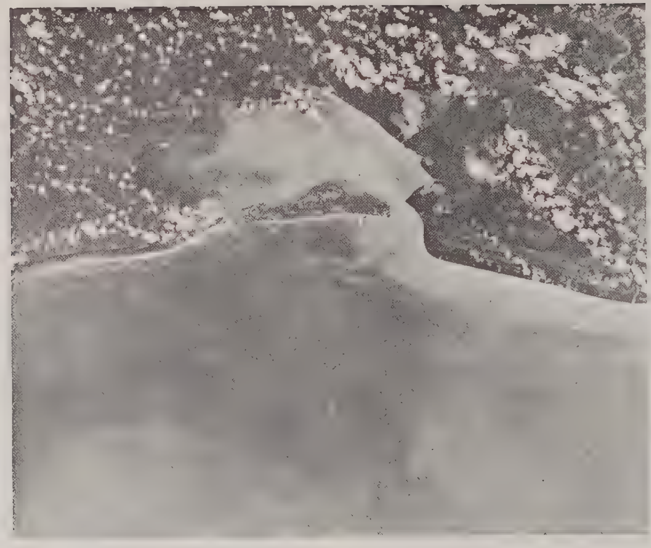

Figure 1. Laguna de Terminos. This photograph was taken during Gemini V, August 22, 1965, at 20:09 GMT from an altitude of 100 nautical miles. A slightly modified Hasselblad 500 C camera with an 80-mm focal length lens was used.

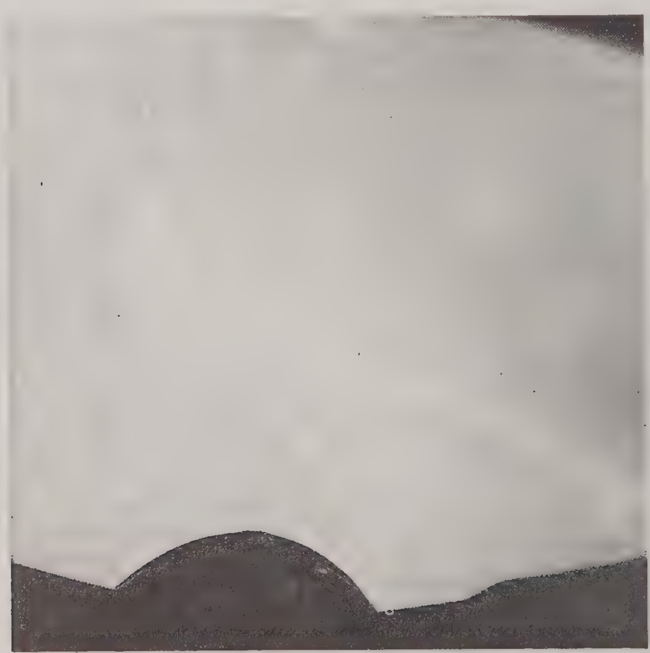

Figure 2. Texas and Louisiana coast. This photograph was taken during Gemini XII, November 14, 1966, at 13:00 hours local time from an altitude of approximately 178 nautical miles. A slightly modified Hasselblad 500 C camera with a 38-mm focal length lens was used.

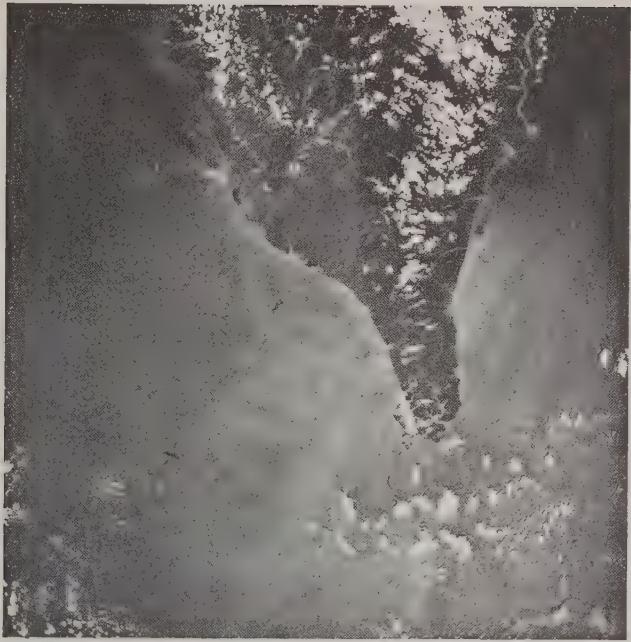

Figure 3. Taiwan. This photograph was taken during Gemini IX, July 20, 1966, at 12:00 hours GCT. A slightly modified Hasselblad 500 C camera with an 80-mm focal length lens was used.

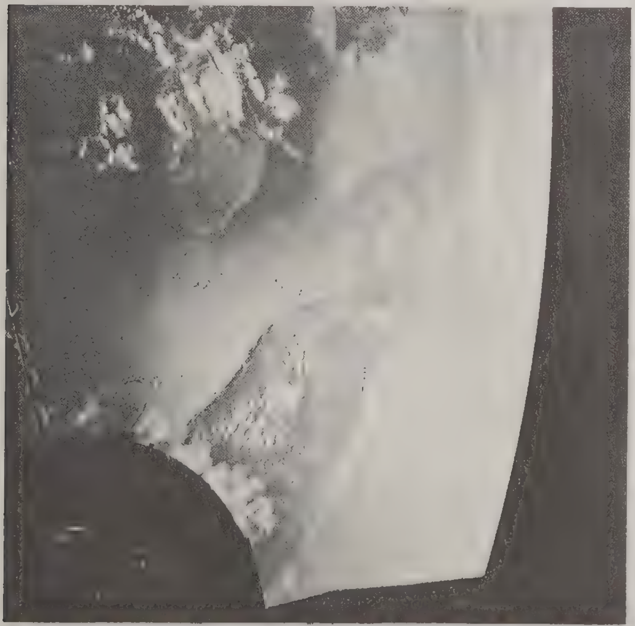

Figure 4. Southern Florida, Bahama Islands, Cuba and Yucatan. This photograph was taken during Gemini XII, November 12, 1966, at 22:31 hours GET from an altitude of 180 nautical miles. A slightly modified Hasselblad 500 C camera with a 38-mm focal length lens was used.

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DOMESTICATING THE SEA: PROSPECTS AND PROBLEMS

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All of you have probably read about the wonders we can expect some time soon from mining the sea, farming the sea, or living in the sea. So I hope you are asking yourselves, "Why talk about domesticating the sea instead of, say, farming it, mining it, or even milking it?" The answer is that I believe that we will have to domesticate the sea before anyone can make a go of farming, living in, or even mining the sea, except in the most primitive and wasteful manner.

The word "domesticate" comes from the Latin *domus*, meaning house, household, or residence. Domestication means adapting a plant or animal to the household. More broadly, it means adapting it to live on man's home grounds, whether these be a cave, a tent, a farm or ranch, or his parlor.

But it means more than that. Domestication implies that man changes his ways to accommodate his new partners, friends, or slaves when he domesticates them. If you doubt this, consider what the domestication of grass into wheat meant to the nomadic tribes of man 12,000 years ago. It meant food which he could store for the winter or for years of drought and famine. But it also meant that he had to settle down to care for his crops. This led to the invention of the city, of landlords and taxes, writing to keep accounts, and finally to that pinnacle of civilization, the freeway traffic jam.

You yourselves have modified your lives in order to live with the domesticated descendant of *Saccharum robustum* and *S. spontaneum*. Your lives have been changed by the fact that some long-ago citizen of New Guinea liked wild sugar cane with his long pig.

So domestication means more than farming the sea, or fishing, or grubbing for clams. It means selecting a wild plant or animal; learning its needs, habits, and preferences; favoring it in its struggle for existence by feeding, healing, and protecting it; suppressing competing forms of life -- as when a farmer weeds; and, perhaps most important of all, breeding it selectively to bring out desired characteristics and suppress unwanted ones. And it means that man himself is willing to adapt his ways to the newly domestic species.

This has been the way of civilization for many thousands of years on land. I believe it is the way we must aim to go if we wish to civilize the sea and not simply plunder it.

But it can be argued that men have been able to extract wealth from the ocean in its wild state for thousands of years. Why should we bother to domesticate it? After all, it will require time, much hard work, a lot of money, some wasted effort, and possibly even a number of lives lost.

For one thing, there is a challenge here. Think of turning the vast and mostly useless ocean into a thriving healthy mixture of farm, pasture, ranch, park, and wilderness, each with its marine equivalents of wheat, cattle, sheep, and poultry -- and even dogs -- to help us herd and hunt and to keep us company. Surely this is something we would be proud to leave our children, and their children's children.

Then there is an even more compelling reason: economics. Domesticating the sea will make men and nations richer and more powerful. What did our ancestors eat, wear, buy, and sell, if not the products of domestic plants and animals: grain, meat, cotton, wool, leather? No economy based on hunting and gathering wild animals and plants has ever been able to compete with one based on farming and herding. The American farmer feeds more than 30 people in addition to himself; he frees these 30 to do other things besides growing grain for their daily bread.

Let's look at the amount of money earned by those industries which extract their raw materials from earth's soil and water. Figure 1 shows the monetary value to the producer in 1964 of gathering and farming of plants, hunting and herding of animals, and of mining. It shows this for land and sea, for the world and for the United States. Gathering and

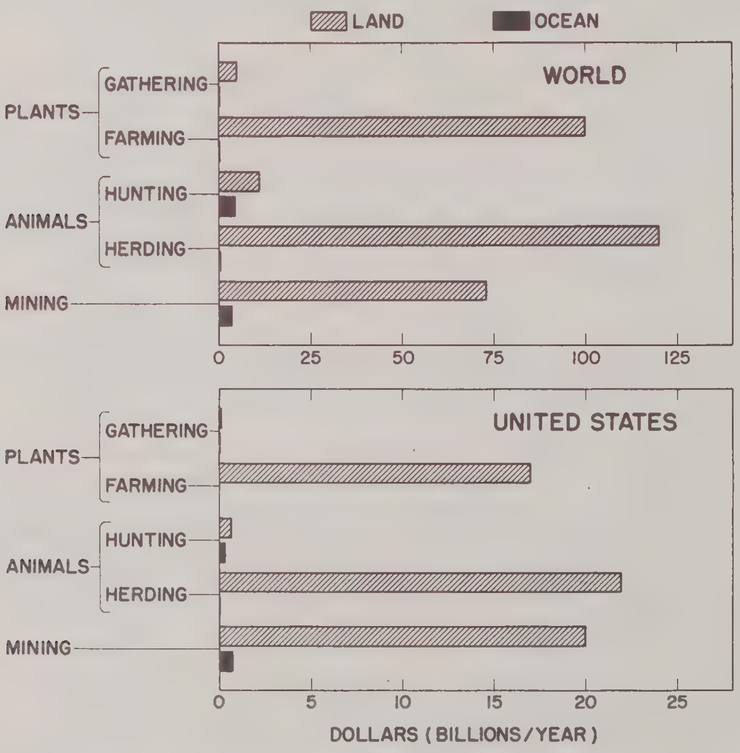

Fig. 1. Dollar value of land and ocean products, world and United States, 1964. (Adapted from table 1, K. O. Emery and C. O'D. Iselin, "Human food from ocean and land", *Science*, 157:3794, Sept. 15, 1967, pp. 1279-1281.)

hunting operate on wild populations, farming and herding make use of domestic plants and animals. Note that for the ocean only hunting and mining produced any appreciable income, about $4 billion apiece. Farming the sea, as defined here, deals only with deliberate cultivation of plants, and this takes place almost entirely in Japan, where various seaweeds are farmed, mostly for flavoring rather than simply for nutrition. Observe that operations involving domesticated land plants and animals brought in from 10 to 20 times as much income as those involving wild populations, on a worldwide basis. In the United States, gathering wild plants and wild animals on land brought less than $750 million to the producer, whereas farmers and herders earned 55 times as much -- $39 billion.

There is yet a third reason for domesticating the sea, a rather grim one which is shown in Figure 2. The upper line shows the world's population as it has grown from 1900 to 1965 with a projection to the year 2000. Below that is the projected demand for protein to feed this population. Note that the amounts per person are much more modest than we are used to. At a subsistence level, each person each year needs about 55 pounds of protein -- some 12 pounds from pulses (peas, beans, and such), 35 pounds from cereals, and 8 pounds from animals. These are bare minimum amounts required to maintain life. Americans consume roughly 20 times as much animal protein as the minimum shown here. In fact, we feed our pigs and cattle better than most of the rest of the world feeds its people. Now I don't feel guilt about this; quite the contrary, it is a marvelous record of accomplishment on the part of our farmers and ranchers. Each nation must accept primary responsibility for feeding and clothing its own population. Our own country, and quite a few others as well, are doing this superbly. Others, obviously, are not.

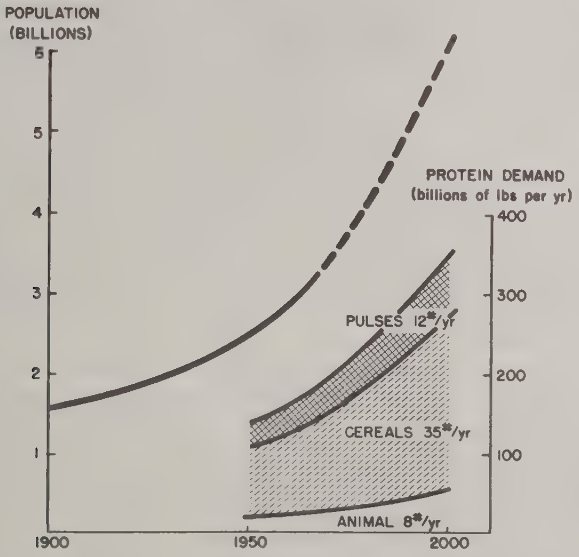

Fig. 2. Projected world population and annual protein demand. (Adapted from table 2.1, "Effective use of the sea", Report of the Panel on Oceanography of the President's Science Advisory Committee, U.S. Government Printing Office, Washington, D.C., June 1966, 144 pp.)

But a clear conscience and lack of direct responsibility will not keep us out of trouble if we stand by with folded hands while millions starve in Africa, Latin America, and Asia. I don't believe that the developed nations can or should feed the hungry nations, except on an emergency basis. But it may be a matter of simple survival for us to show the hungry nations how to feed their own people. At least we may need to do so until the real problem is solved. That is not one of feeding the world's population, but one of finding acceptable ways to keep that population within tolerable bounds.

By now you may be willing to consider that the sea is worth domesticating, that such a course may be desirable on economic, political, and social grounds, and as an intellectual challenge. To do so will allow us to make wise use of the last remaining major resource on our ravished planet. How are we going to go about it?

There are degrees of domestication, as anyone knows who has shared a home with a dog, a cat, and a wife. Wheat and corn are domestic, as are some strains of yeast. Corn, in fact, could not survive without the hand of man to plant and care for it, because it has lost its ability to broadcast seed. Animals like the chicken and the dog are very much domesticated. But there is very little difference, if any, between most wild trees and a domestic tree of the same species grown deliberately by man. The line between wild species and domesticated ones is not always clear. It depends upon our own attitudes as well as the plant's or animal's response to our care. Let us see if we can learn something from the history of domestication.

There are some 1,100,000 species of animals on our planet. Of these, 85 percent are insect species, and only a couple of these -- the honey bee and the fighting cricket occur to me offhand -- are domestic animals. That leaves 200,000 noninsect species. Of these, I would estimate that less than 100 have become domesticated. My own list comes to about 30 animals, which we raise for food, as draft animals, beasts of burden, hunting animals, or as pets. Only 1 in 10,000 has been selected by man to share his home grounds. And most of these are fairly close relatives of his, vertebrates or even mammals. I haven't even tried to list domestic plants, which range from the microscopic yeast cells which we breed for baking or brewing, to giant fruit trees which we plant, graft, and prune to our liking. These also represent but a tiny fraction of all the species which grow on our planet. According to the Rockefeller Foundation, only about a dozen out of some 12,000 known species of plants supply most of mankind's food. So, first of all, domestication is a process of selection. Only a very small percentage of the existing species of plants and animals have been chosen to keep man company.

Domestication seems to have begun in earnest about 10,000 B.C., when the first traces of deliberate agriculture appear in the archeological record. And it was completed, for the most part, well before the time when written records first appear. So we don't know how it came about. I suspect that it was a subtle process, only partly conscious or deliberate, and that it involved little brute force. Instead, it demanded a profound intuitive understanding of the requirements of each species being domesticated. At least, this is what we find today when taming or trying to raise a wild or partially wild animal.

One particularly interesting example took place in the local Bureau of Commercial Fisheries Laboratory a few years ago. No fish in the sea is wilder and less domesticated than the skipjack tuna or aku, which make up the bulk of the commercial catch in Hawaii. Researchers at our Laboratory and at the University of Hawaii were trying to keep aku alive in captivity to study their behavior and their ability to see and hear. But the animals they caught invariably died after 1 or 2 days, usually with large bruises on their bodies -- some of them perfect outlines of a man's hand. After 2 years of experiments, Eugene L. Nakamura of our Laboratory found the secret. The aku are very active animals and generate a lot of heat in their muscles. Nature apparently took care of this by giving the aku an extensive system of blood vessels just below the skin, which would help carry the excess heat out of the muscles and transmit it to the water. It turned out that the high mortality among the captured aku was due to internal hemorrhaging when these blood vessels just below the skin were damaged as the fish were handled in nets or by hand during capture, and during the transfer from the ship's baitwells into the holding tanks ashore. The secret of keeping captive aku alive was simple: You just could not touch them or let them touch anything.

Mr. Nakamura built small portable tanks to take along on our research ships. The fish were caught, lifted out of the water with the pole and line, and then gently lowered into the portable tanks, giving them slack line which lets them shake the barbless hook and swim free in the tank. When the ship got back to our facility at Kewalo Basin, these tanks were lifted off the ship, with the fish and water still in them, and were taken to the holding tank area. Each portable tank, with one to six aku in it, was then lowered into the holding tanks, and a door in the side of the portable tank was opened to let the fish swim out. The only thing they ever touched was the fish hook. Instead of dying within hours, with bloody bruises under their skins, these fish lived for months and even for a year or longer, and became rather tame. We still don't know why they die after 6 months to a year, but this time it looks like some sort of deficiency in their diet. Still, they live long enough to provide us with useful information on their swimming, their feeding and schooling behavior, their ability to see, and their hearing.

So, man has to select an animal or plant and learn a great deal about it, before he can domesticate it. What else is required? Nothing, really, except patience. And one more thing, very vital indeed: a particular attitude or frame of mind. There must be a desire to take care of the animal or plant, as a population, and not simply make use of it. Keeping breeding stock, or a store of seed grain, is one way to think of it. A sense of property is another way to look at it. This is the single key difference in the way man behaves toward a wild plant or animal as compared with a domestic one. The domestic one belongs to him, and he must care for it. The wild one belongs to nobody, and a man had better get his share before someone else gets to it first.

Keeping breeding stock, or a store of seed grain, leads towards genetic selection. In wild populations, genetic selection works against man's interests, because we select the best stock and remove it, thus putting unfavorable selective pressure on the population.

In northern Japan, there is a fishery for a type of crab called samurai crab. Many years ago, according to G. Evelyn Hutchinson, a small proportion of this population of crabs was found to have a mutation which resulted in a minor change in the pattern of markings on its shell. Maybe one in several hundred crabs showed this odd pattern, which strongly resembled a skull or death's head. Either because of their own superstition, or because of superstiticus customers who would not buy such crabs, the fishermen threw these mutated animals back while keeping the rest. Today, most of the crabs that are caught in this fishery have the skull pattern on their shells, because such a pattern helped them to survive under the pressure of fishing mortality.

Off California in the 1930's there was a large fishery for the California sardine, centered in the area between Monterey and San Pedro. Today, this industry is dead because the sardine has almost vanished. In its place we now find a similar species, the anchovy, which is not so commercially desirable. Why? There is no final answer as yet, but at least two factors may have been important. Minor changes in the ocean offshore resulted in poor reproduction by sardines over a period of several years. Continued pressure from the fishery during those unfavorable years may have been the final straw that allowed a weed species, the anchovy, to move in and take over the sardine's territory.

These two examples of selection by man acting on wild populations stand in strong contrast to your own experience with the domestic species of sugar cane and with the way in which man treats other domestic species. Selective breeding has resulted in varieties which produce higher yields, which are more resistant to disease and natural disasters such as drought or flood, or which ship better or bring better prices in the marketplace.

What domesticated species do we have in the ocean? Almost none. The porpoise may be domesticated soon, and it may play the role of the dog, helping us to herd and hunt, and keeping us company in the sea. But the first honors probably go to the Japanese oyster industry, which began selective breeding more than 40 years ago. Improved stock and better production methods have brought astonishing benefits. From production of about 600 pounds per acre per year, the yield has been increased to 16,000 pounds or more, an increase of 26 times!

Dr. Lauren Donaldson at the University of Washington is another veteran of this game. He has concentrated upon selective breeding of trout and salmon. Donaldson's trout are famous; by breeding for size he has managed to obtain trout which are more than twice as long as the wild strains, and weigh four or five times as much. Donaldson's salmon are the result of more recent work. The salmon he worked with normally spend the first year of their lives in fresh water streams and ponds, then migrate to sea, where they remain another 4 years. The survivors return at age 5 to the grounds where they were spawned, to reproduce their kind and die. Donaldson reared his fish in a laboratory pond through their first year, marked them by clipping parts of their fins, and then sent them on their way. Perhaps 1 to 2 percent returned, most of them after 4 years. But a very few came back in 3 years. The largest of the early fish were then selected for breeding, and the process repeated. When I left Seattle 7 years ago he had a strain of salmon which called his laboratory "home", and which returned in 3 years, sometimes 2, but were as big as normal 5-year-old fish. Most important of all, the losses due to natural mortality during that fourth year were avoided, and instead of 1 or 2 percent of the yearlings returning as adults, there were returns of 5 to 10 percent. And they swam right into his laboratory pond! If he can manage to get the fish to return after only 2 years, he may reduce mortality to such an extent that 10 to 20 percent returns would be commonplace, a tenfold increase in survival.

So domestication of marine animals is clearly possible, and should be very much more profitable than our present practice of harvesting wild species.

What I would propose is that we, as a nation, make a concentrated effort to select marine species for domestication, and learn how to grow them, breed them, and care for them.

Where should we do all this? As on land, there are areas of the sea favored by nature, and it is in these that we are most likely to achieve success. Figure 3 shows the way in which productivity varies throughout the world's oceans. The most productive areas are the west coasts of North and South America and Africa, and the higher latitude mid-ocean areas from Japan to Canada, New England to Norway, and the Antarctic Ocean. The richest areas --off Peru, South Africa, and the southern Atlantic -- yield about 50 to 60 tons of plant matter per acre per year. The average for all oceans is about 10 tons per acre per year. Desert areas such as that in which Hawaii is located yield perhaps 2 to 4 tons per acre yearly. Compare this with 50 tons of cane per acre produced each year in Hawaii, and you will see that the best intensive agriculture produces about as much as the best which nature achieves in the sea.

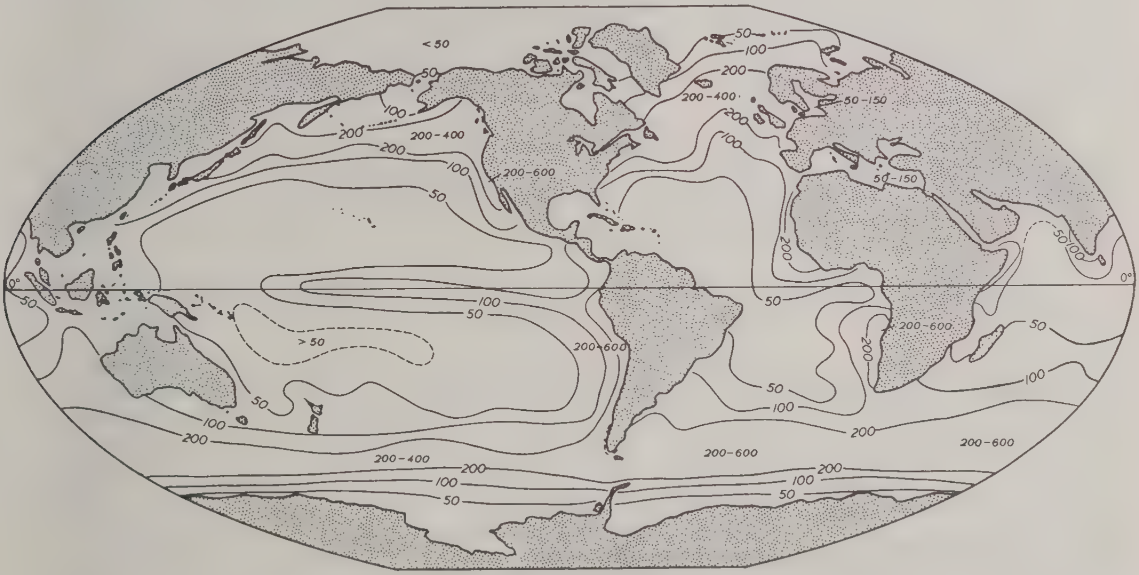
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Fig. 3. Estimated annual photosynthetic productivity of the oceans; units: grams of carbon/meter^2/year. (From R. H. Fleming, "General features of the oceans", Memoir 67, Vol. 1, Geol. Soc America, 1957, pp. 87-108.)

But marine plants are not sugar cane. For one thing, they are rootless, drifting, tiny single-celled plants with a lifetime of a day to a week. For another, most are enclosed in chalk or silica (glass) cases, which make them gritty food. Only a very few marine plants show any promise as food for mankind, and almost all of these grow on the bottom in shallow areas of the sea. It is a reasonably safe bet that the Japanese will remain the only true farmers of the sea. The wealth of the sea is in its animals, not its plants (although some marine plants may be extremely valuable for some special purposes, such as medicines and drugs).

The animals which feed on these tiny plants, the grazing animals called zooplankton, stay pretty close to the pastures, which you saw on Figure 3. It takes some 10 pounds of plant cells to grow 1 pound of grazing animals, so the richest areas you see here should produce roughly 6 tons per acre of small, shrimplike crustaceans annually, most of them the size of a match head or smaller. The largest, the krill, are as much as 1 inch long, and serve as food for the largest animals on earth, the baleen whales.

The biggest fishery in the world, the Peruvian anchoveta fishery, is obviously located in a very rich zooplankton area. Other rich areas are the Grand Banks, Iceland, the salmon areas of the North Pacific, the waters of Southeast Asia, Western Australia and Africa, and the entire Antarctic Ocean north of the pack ice. In these rich areas, something like 1,000 pounds of fish are produced per acre each year. In desert areas such as the central North Pacific around Hawaii, 20 pounds per acre per year is a more likely figure. If we speak of tuna such as the skipjack, which feed still higher on the food chain, we might expect our part of the world ocean to produce some 2 pounds of tuna per acre per year. Fortunately for the tuna industry, there are a lot of acres of water in the central Pacific.

Compare these figures with those for the best Hawaiian sugar land, which has yielded as much as 20 tons of sugar per year. Pound for pound, sugar land is 10,000 to 20,000 times as productive as the ocean near here, if all that we take out of that ocean is the larger predators such as tunas and marlins.

Perhaps we could do better if, instead of fishing for wild tuna, we grew domestic ones, fertilizing the water to make it a better "pasture"

For my own amusement I made some calculations on this. Suppose, after seeing another re-run of "Sea Hunt", that we decide to set ourselves up as fish ranchers. We lease a 100-square-mile area just west of Lahaina on Maui from the State, fence it with fish netting, and decide to raise sashimi on the fin, so to speak. Our "ranch" has 80,000 acres, about as much area as the land devoted to sugar cane on the island of Hawaii. Our fence has to be, not 10 feet high, as on land, but 300 feet deep and over 40 miles long. So it costs us, all told, about $8 million or $100 per acre. Fertilizer and manpower might cost another $50 per acre per year. What we propose to do is to trap small tuna, keep them 1 year while they grow about 20 percent in our enriched "pasture", and then sell them to the cannery. This saves us the time and trouble which would be required to raise the fish from selected parent stock. We are trying to bypass domestication, in other words. Under the very best conditions, if we were able to boost productivity to that of your sugar land and convert everything into growth of our captive tuna, we might add 1,000 pounds per acre per year to the weight of the tuna. At $0.10 a pound, we would gross $100 in sales on $150 of capital and operating costs -- not bad.

At this point I was wondering whether I shouldn't quit my job and start the tuna ranch going. Alas, there is a catch. Natural fish populations have a pretty high mortality rate, which runs around 25 to 50 percent per year. Unless we can cut that drastically, we would have to catch $750 to $1,000 worth of tuna to start with, feed them 1 year, and then sell the survivors for about $600 -- a guaranteed net loss of $150 to $400 per acre, minimum, in our ranching operation.

This little example simply serves to point out the inefficiency of trying to deal with natural populations. Ranching requires the use of domestic animals, with low mortality rates and high efficiency for conversion of food into meat.

To sum up: Civilization has gone hand in hand with domestication of land plants and animals. We might even say that man and his domestic species civilized each other. Today domestic plants and animals yield 25 to 50 times as much to mankind as wild plants and animals. Man husbands and cares for his domestic plants and animals. He improves them by genetic selection and helps them along by weeding out competitors. And man adapts himself to the needs of his domesticated partners.

In contrast, wild plants and animals belong to no one, and are therefore plundered instead of being cared for. Man's attitude toward wild things results in adverse genetic selection by removing the best and leaving the worst behind. He also leaves the weed species alone, so that they often move in to finish the job of eliminating desirable wild plants and animals, after man has taken his toll.

It therefore seems to me that we must domesticate the sea if we are to use it wisely. We should start to choose those animals, and perhaps a very few plants, which might prove of most value to us when domesticated; we should learn as much as we can about them, their needs, diseases, preferences, and their competitors. From this group we can then select a small number which will form the basis for a complete, diversified economy in the sea. In a few generations, the result would be a balanced, healthy mixture of farm, pasture, ranch, park, and wilderness, capable of feeding and providing a living for generations of man yet to come.

The alternative, it seems to me, is to stand by and watch man rob, plunder, pollute, and lay waste his last remaining resource on this small planet.

Our children's children will have to live with the results. The choice is ours to make.

The Kuroshio-Oyashio Front as a Compound Vortex Street[1]

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ABSTRACT

A concept presented in this paper can account for a wide variety of observed features in the Kuroshio-Oyashio front, just east of Japan. The concept, a synthetic description, consists of two von Kármán vortex streets arranged side by side; it is referred to as a compound vortex street. Von Kármán's kinematic theory is generalized to include all possible vortex-street arrays. Observations of sea-surface currents and mass transport in the Kuroshio-Oyashio front show reasonably good quantitative agreement with the theory; also, there is qualitative agreement between the model and the observed distributions of temperature and density in the region.

Introduction. The front where the Kuroshio and the Oyashio currents meet, just east of Japan, is one of the most interesting features of the Pacific Ocean. To the biologist it is a zone of high productivity, the site of several major fisheries, and a boundary where many diverse organisms congregate. To the descriptive oceanographer the front is a boundary between the warm saline North Pacific Central Water mass and the cold dilute Subarctic Water

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mass. Dynamically, the front can be considered as a band of concentrated kinetic energy separating two regions having different potential energy. Biologically, chemically, and physically, the region displays marked contrasts and sharp gradients. Thus it is not only interesting but very complex.

This complexity makes it difficult to provide an unambiguous description of the Kuroshio-Oyashio region, even though relatively large amounts of data are available, at least for the western and southern portions of the region. Its analogue in the Atlantic, the eastern extension of the Gulf Stream off the North American coast, presents similar problems. Working with a single set of near-synoptic observations in that area, Fuglister (1955) was able to develop three dissimilar yet plausible interpretations of the temperature data. Stommel (1958: 60) noted that "the chief features are so poorly known that a serious theoretical analysis of the Gulf Stream cannot be made at present." Better descriptive models of the Gulf Stream and the Kuroshio would help to reveal the order underlying their complexity and would make it possible to conceive new theoretical approaches and improve the design of data collection at sea.

One such model, an elaboration of the vortex street concept first developed by von Kármán (1911) in his classical theoretical discussion of periodic wakes, is presented here. The model originated as an empirical concept to guide the contouring of depth, salinity, and dissolved-oxygen values on a series of charts of isopycnal surfaces in the "Oceanographic Atlas of the Pacific Ocean" (Barkley 1968).

In the following account, a variety of charts is presented as empirical evidence for the presence of a vortex-street system east of Japan. Following is an analysis that shows that the vortex street concept has some degree of quantitative theoretical validity. A discussion of the implications derived from the model in terms of theory and observation makes up the final section.

The model, an oversimplified but apparently accurate synthetic description, fits a variety of observed data to such a degree that it should probably be considered as a useful hypothesis to be tested by field work and theoretical studies.

The Compound Vortex Street. Authors considering theoretical models of meanders in ocean-current systems have largely concerned themselves with systems in which the current is represented by a single high-velocity core (Stommel 1958, Fofonoff 1962, and Ichiye [unpublished ms]). Their solutions have usually taken the form of wavelike disturbances in the axis of this core. Although such theoretical models appear to account for certain observed conditions in the Gulf Stream and the Kuroshio where these currents flow along western coastal boundaries, they do not adequately describe conditions that exist after the currents leave the coast. In these offshore areas there is considerable evidence of multiple high-velocity cores separated by weaker countercurrents (Fuglister 1951, 1955); for such areas, more complex models must be considered.

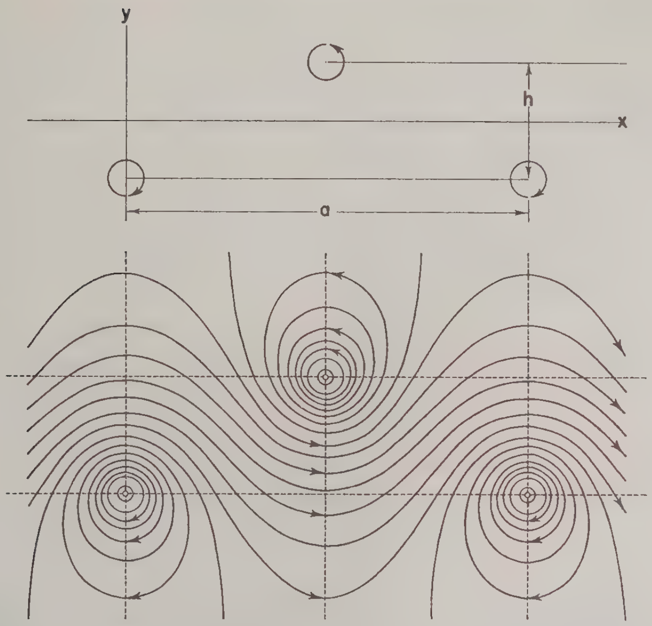

Figure 1. Von Kármán vortex street.

Upper panel: Schematic diagram showing coordinate system. *a*, wavelength; *h*, distance between vortex rows.

Lower panel: Streamlines for a von Kármán vortex street, from Tietjens (1934). Contour interval (not given in the original) estimated at 0.025 unit of ψ/k.

The simplest model that appears capable of representing the meanders, eddies, and countercurrents near the Kuroshio-Oyashio front is a configuration that resembles a pair of von Kármán vortex streets arranged side by side; this configuration is here termed a compound vortex street. Von Kármán vortex streets (or wakes) are a type of flow that is characterized (Goldstein 1938) by a double row of vortices, those of one row having positive (cyclonic) circulation, and those of the other, negative (anticyclonic) circulation. Fig. 1, upper panel, shows this arrangement, which has a wavelength, or pitch, *a*, and a spacing between rows, *h*. The lower panel in Fig. 1 (from Tietjens 1934) shows the streamlines for a single vortex street.

If we add together two identical single vortex streets, displaced $a/2$ unit right or left with respect to each other, so that the array is symmetrical with axes spaced $2h$ units apart, we obtain the streamlines of the compound vortex street shown in Fig. 2. An infinite number of combinations can obviously be obtained by varying the distance between adjacent vortex streets and their relative phase; however, the Kuroshio-Oyashio front apparently tends to assume only two configurations: a symmetrical compound vortex street similar to that in Fig. 2, or, more seldom, a single high-intensity vortex street similar to that in Fig. 1.

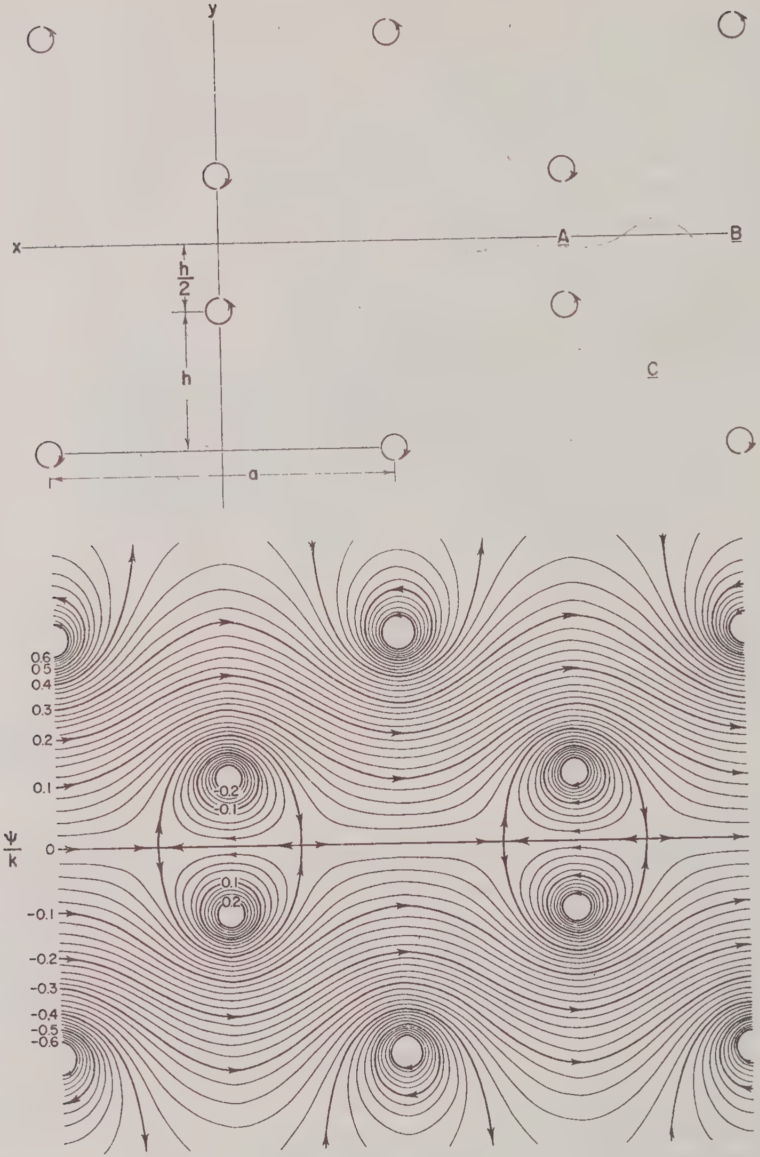

Figure 2. Compound vortex street.

Upper panel: Schematic diagram showing coordinate system. a, wavelength; h, distance between vortex rows; A, B, C, midpoints between vortex centers (see text).

Lower panel: Streamlines for a compound vortex street, from (6). Contour interval: 0.020 unit of ψ/k.

Observations on Compound Vortex Streets Near Japan. To apply the vortex-street model to oceanographic data, we assume that the flow is steady, frictionless, and geostrophic, so that the streamlines in Fig. 2 might represent isotherms as well as currents, the topography of an isopycnal surface or idealized thermocline, or the dynamic topography of the sea surface.

On this assumption, in the Northern Hemisphere we can consider the streamlines in Fig. 2 as:

(i) An idealized set of isotherms, with the uppermost row of vortices representing a series of temperature minima, the next lower row representing temperature maxima, the third row representing minima, and the fourth row representing maxima.

(ii) An idealized set of isobaths representing the topography of a sigma-t surface or simplified thermocline, in which the upper row of vortices represents elevations or domes and the next represents depressions; the lower half of the figure is a mirror image of the upper.

(iii) The idealized dynamic topography of, say, the sea surface relative to 1000 decibars; here the upper row of vortices would appear as minima in the dynamic topography, the second row as maxima, etc.

We can now consider charts of the Kuroshio-Oyashio front showing temperature, topography of isopycnal surfaces, dynamic topography, and surface currents, in terms of the simple model represented by Fig. 2.

Temperature at 200 m and Surface Currents. Fig. 3 (upper panel) shows part of a chart of the temperature at 200 m for July through September 1961. The chart was prepared by the Japanese Hydrographic Division, Maritime Safety Board (Vol. 2, 1960–1964). Fig. 3 (middle panel) interprets the isotherms in terms of the compound vortex-street model. This interpretation is based primarily upon the positions of temperature maxima and minima (represented by + and – signs in the middle panel of Fig. 3) and secondarily upon the shape of the temperature contours, since somewhat less subjective interpretation is required for proper positioning of a point than of a line. Interpretation of the original temperature data in terms of the compound vortex street would require a few changes in the contours on Fig. 3, particularly near 39°N, 147–148°E, where the contours are based on a small number of widely spaced observations. If Fig. 2 were used to represent the isotherms in the upper panel of Fig. 3, the central axis would have a temperature of about 8°C and the contour interval would be approximately 0.3°C.

The model implies that westerly countercurrent flow should be present along 38°N, at approximately 143°E, 147°E, and 152°E. The corresponding current chart in the same atlas, presented in somewhat simplified form in Fig. 3 (lower panel), shows strong evidence of the westerly flow predicted by the model, with maximum values of westerly flow of 1.2, 1.0, and 0.4 knot, respectively, at the three locations. Many other features of the observed current pattern also fit the model, although a number of exceptions are evident. In Fig. 3 the wavelength of the compound vortex street is about 4.5° of longitude.

The two volumes published by the Japanese Hydrographic Division, Maritime Safety Board contain quarterly charts for the period 1955–1964. Only

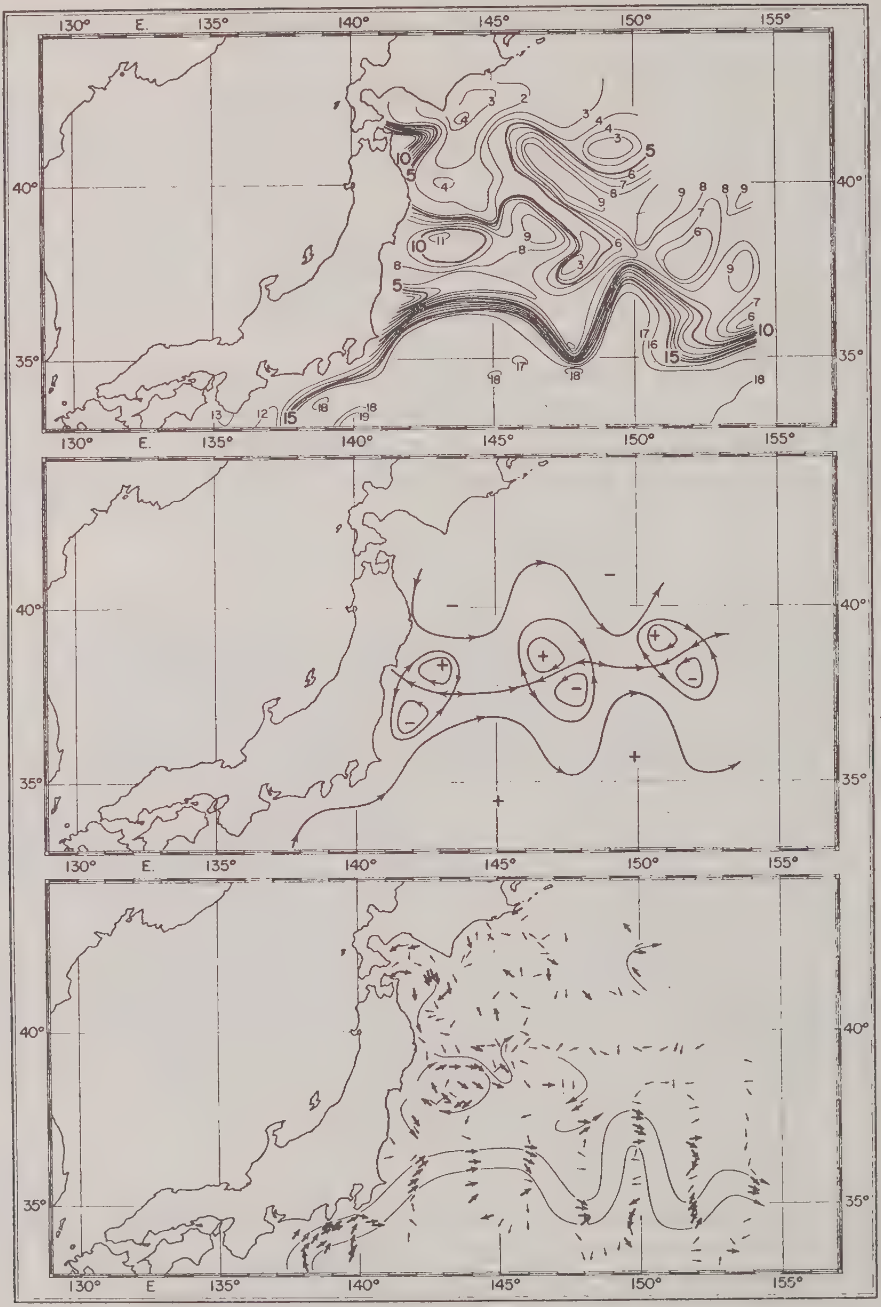

Figure 3. Upper panel: Temperature (°C) at 200 m off Japan, July-September 1961.
Middle panel: Interpretation of upper panel in terms of the compound vortex-street model. Temperature maxima and minima labeled + and –, respectively.
Lower panel: GEK current observations, July-September 1961. Light arrows, velocities of less than 1 knot. Heavy arrows, velocities of 1 knot or more.

Source of data: Japanese Hydrographic Division, Maritime Safety Board (Vol. 2, 1960–1964). Reduction in scale from the original charts made it necessary to simplify the lower panel by omitting numerical velocity values, by modifying the symbols used, and by omitting a few observations of weak currents (0.5 knot or less) in coastal regions where many observations were made.

23 of these charts cover enough of the area east of Japan for inclusion of at least one wavelength (*a* in Fig. 2, approximately 4.5° of longitude, or 400 km) of the compound vortex street. Sixteen of these 23 charts show evidence of compound vortex-street systems as determined by the presence of at least two pairs of low-high temperature "couples" (corresponding to the inner vortices of the model) between the two major temperature gradients on charts of the 200-m temperature in the region of the Kuroshio-Oyashio front. Four other charts suggest the vortex-street phenomenon, but the data are not conclusive. Finally, three charts show no evidence of vortex streets; these charts are for the first, third, and fourth quarters of 1958; the chart for the second quarter of 1958 is considered to be inconclusive. A possible connection between the compound vortex-street system and the cold eddy near 138°E off the southern coast of Honshu is suggested by the fact that—as judged from the 200-m temperature charts—this eddy was weak from the fourth quarter of 1957 through the third quarter of 1958 (entirely absent during the second quarter of 1958), a period when no compound vortex-street system was evident east of Japan.

Density Surfaces. The upper panel in Fig. 4 shows, for the area near Japan, the topography of the 26.80 sigma-t surface for the July-September quarter (Barkley 1968). Vortices occur as isolated depressions and elevations (represented by + and – signs in Fig. 4, lower panel) in the depth-contour pattern for this surface. Fig. 4 (upper panel) also shows numerical values of the maximal or minimal depths at the center of each vortex. Note that east-west rows of vortices of the same type tend to have similar maximal or minimal depths. Averages of oceanographic station data within areas 1° of latitude by 1° of longitude form the basis for the upper panel.

The contours in the upper panel of Fig. 4 were obtained by using the model as a guide, wherever the data permitted ambiguous interpretations. It is therefore possible that some of the details of the contours may represent bias in favor of the model. However, the four east-west rows of isolated eddies would appear as such in any analysis.

The lower panel of Fig. 4 presents an interpretation of the topography of the 26.80 sigma-t surface in terms of the compound vortex street. The three or more wavelengths present have similar features that recur at intervals of 4° to 5° of longitude, or about 370 km. If Fig. 2 were used to represent the isobaths in Fig. 4, the central axis would lie at a depth of approximately 300 m and the contour interval would be about 10 m.

Dynamic Topography. Very few charts that show details of the dynamic topography of the sea surface just east of Japan have been published. Perhaps the best of them are the three presented by Ichiye (1957); these are reproduced in Fig. 5. No clearcut evidence can be found on these charts in favor of or

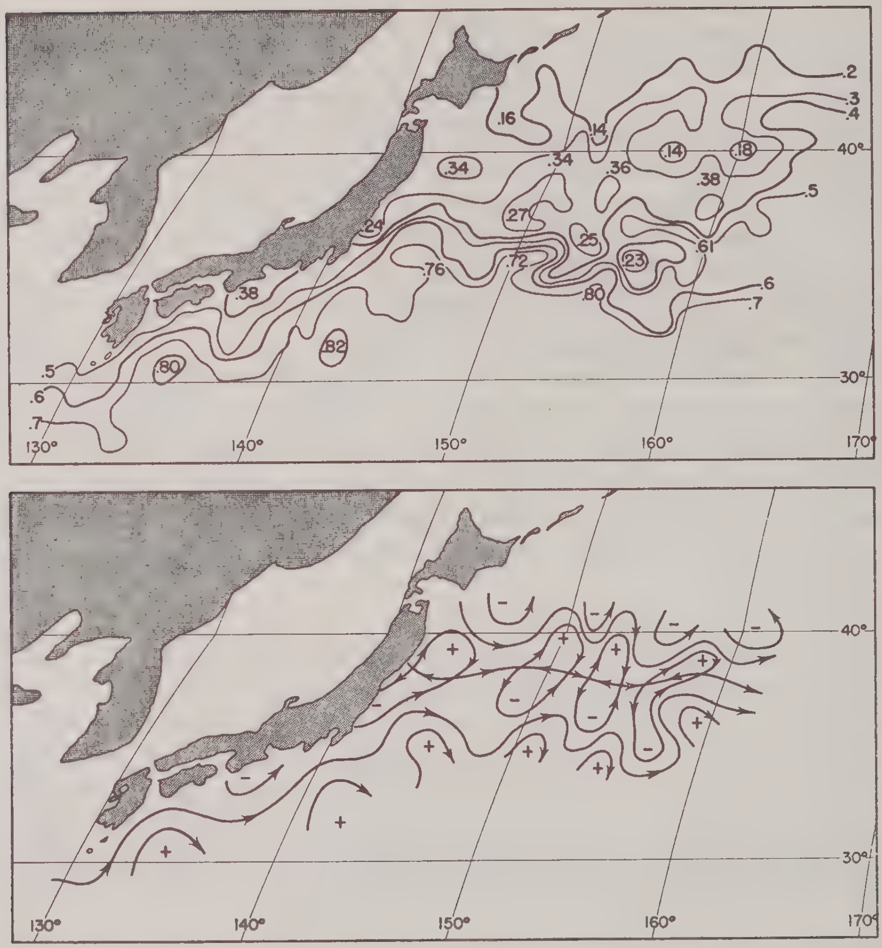

Figure 4. Upper panel: Average topography (depths in km) of the 26.80 sigma-t surface for the July-September quarter for all years. Averages by 1° × 1° areas. Maxima and minima in the depth of the surface are shown numerically.

Lower panel: Interpretation of upper panel in terms of the compound vortex-street model. Maxima and minima in the depth are labeled + and –, respectively.

against the presence of internal eddy pairs of the type implicit in the compound vortex-street model. However, there is some indication of such an eddy pair in the lower panel of Fig. 5, and the upper panel shows some flow with a westward component near 38°–40°N. The middle panel lacks any such eddies or countercurrent flow near the Kuroshio-Oyashio front.

It is notable that the middle panel of Fig. 5 represents a period when the cold eddy south of Honshu was almost absent whereas the upper and lower panels represent conditions at times when this cold eddy was well developed. The isotherms on the original charts (not reproduced in Fig. 5) show that a single front was present during the period represented in the middle panel,

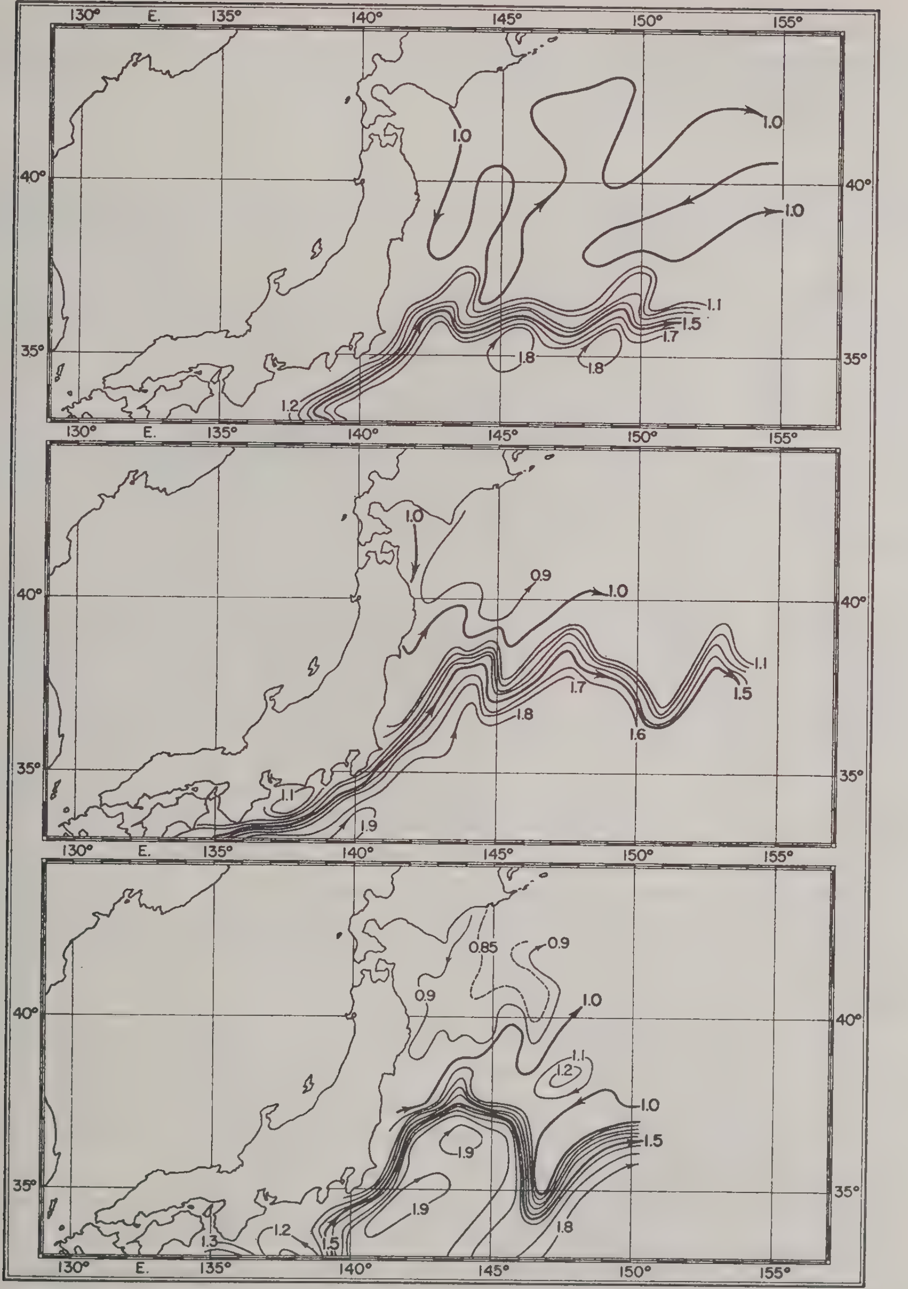
130°
E.
135°
140°
145°
150°
155°
40°
35°
1.0
1.0
1.0
1.1
1.5
1.7
1.8
1.8
1.2
0.9
1.0
1.0
1.1
1.5
1.7
1.8
1.6
1.1
1.9
0.85
0.9
0.9
1.0
1.1
1.2
1.0
1.9
1.5
1.9
1.8
1.3
1.2
1.5

Figure 5. Dynamic topography of the sea surface with respect to 1000 decibars, from Ichiye (1957). Upper panel: August 1939. Middle panel: May-June 1951. Lower panel: May 1955.

but dual systems of fronts, similar to those shown in the upper panel of Fig. 3, were present at the times represented in the upper and lower panels of Fig. 5. These observations lend some support to the idea that a weakening of the cold eddy south of Honshu, as in 1951 and 1958, may coincide with the presence east of Japan of a single vortex street similar to that in Fig. 1 instead of the compound vortex-street system shown in Fig. 2.

SURFACE CURRENTS. Charts of sea-surface currents in the Kuroshio-Oyashio region (e.g., Fig. 3, lower panel) provide some additional support for the compound vortex-street model. Charts of GEK measurements made in that region by the RYOFU MARU (Japan Meteorological Agency 1964: 22, for example) often show isolated areas with westward-flowing countercurrents near 37°–39°N at intervals of 4° to 5° of longitude east of Japan, as the model suggests. These regions of westward flow seem to occur where the high-velocity cores are farthest apart, as required by the compound vortex-street model. These features are also present in the quarterly surface-current charts (Japanese Hydrographic Division, Maritime Safety Board, Vols 1 and 2); Fig. 3, lower panel, is an example.

Theoretical Analysis. The classical theoretical analyses of single vortex streets by von Kármán (1911) and von Kármán and Rubach (1912) as well as subsequent studies summarized by Lamb (1932) and Goldstein (1938) have provided valuable insight into the nature of fluid drag, into the behavior of periodic wakes, and into other related phenomena in real fluids, despite the idealized conditions assumed in the theoretical work. This success suggests that the analysis could usefully be extended to examine the characteristics of compound vortex streets and their implications in oceanology. However, the results must be viewed with caution when applied to the Kuroshio-Oyashio front, because factors that may be important there, such as the Coriolis force, the density stratification, and the effects of lateral boundaries and bottom topography, are not included in this theory.

The classical theoretical analysis assumes that, at a given instant, vortices are present, fully formed, in some specific geometric array. It computes the effects of each vortex on all neighboring vortices to determine an instantaneous field of flow, which in turn determines the immediate subsequent motions of the center of each vortex in the array.

Each circular vortex is assumed to have tangential velocity only, given by $V = k/2\pi r$, where k is the strength (positive for cyclonic rotation) and r is the radial distance from the center. This assumption yields a singular point with infinite velocity at the center of each vortex; consequently, this simple irrotational model lacks physical significance near the immediate center of each vortex.

An infinite row of identical vortices, spaced at intervals of a units along the x-axis, sets up a velocity field whose components in the x and y directions are given by (Lamb 1932):

$$u = -\frac{k}{2a}\,\frac{\sinh\left(\dfrac{2\pi y}{a}\right)}{\cosh\left(\dfrac{2\pi y}{a}\right) - \cos\left(\dfrac{2\pi x}{a}\right)}, \quad v = \frac{k}{2a}\,\frac{\sin\left(\dfrac{2\pi x}{a}\right)}{\cosh\left(\dfrac{2\pi y}{a}\right) - \cos\left(\dfrac{2\pi x}{a}\right)}. \qquad (1)$$

The row remains stationary with respect to the coordinate system, since all the vortex centers are located at points where the effects of vortices to the right and left cancel.

Integration of the equation for v in (1) with respect to x, holding y constant, yields the stream function for a vortex row:

$$\psi = \frac{k}{4\pi}\, ln \left[\cosh\left(\frac{2\pi y}{a}\right) - \cos\left(\frac{2\pi x}{a}\right)\right] + \psi_0. \qquad (2)$$

The resulting pattern of streamlines is shown in Fig. 6.

Equations (1) and (2) form the basis for theoretical discussion of single and compound vortex streets, which can be considered arrays of two or more rows arranged in parallel. The velocity of translation of each row in an array can readily be computed as the sum of velocities induced at the vortex centers by all other rows. Thus, for example, von Kármán (1911) has shown that each row in a single vortex street (Fig. 1) indices a velocity in the vortex centers of the other row:

$$U = \frac{k}{2a}\tanh\left(\frac{\pi h}{a}\right), \quad V = 0. \qquad (3)$$

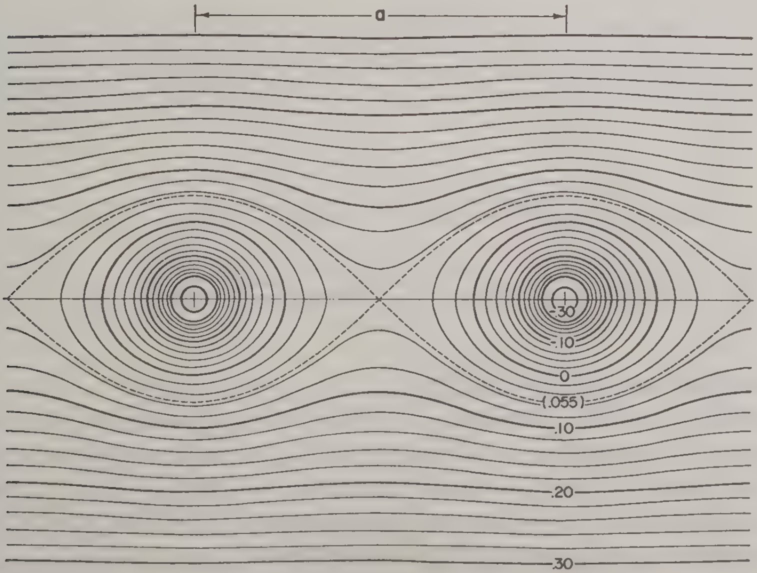

Figure 6. Streamlines for a vortex row, from (2). Contour interval 0.020 unit of ψ/k.

Since the signs of both k and h are opposite for the two rows, U has the same sign for both rows, and the vortex street moves as a unit with the velocity given by (3). Similarly, the streamlines of any array of vortex rows can be obtained by adding together the stream functions (2) of the component rows. For the von Kármán vortex street (Fig. 1), the streamlines are given by the stream function

$$\psi = \frac{k}{4\pi} \ln \left[\frac{\cosh \frac{2\pi}{a}\left(y - \frac{h}{2}\right) + \cos \frac{2\pi x}{a}}{\cosh \frac{2\pi}{a}\left(y + \frac{h}{2}\right) - \cos \frac{2\pi x}{a}} \right]. \tag{4}$$

We can now consider the case shown in Fig. 2, where four rows of vortices rotate in alternate directions. Addition of the velocities induced in the centers of each row by all other rows (1) gives the self-induced velocities of translation of the array:

$$\left.\begin{aligned} V &= 0 \\ U_{\text{inner}} &= \frac{k_o}{2a}\left(\tanh \frac{\pi h}{a} + \tanh \frac{2\pi h}{a}\right) - \frac{k_i}{2a}\left(\coth \frac{\pi h}{a}\right), \\ U_{\text{outer}} &= \frac{k_i}{2a}\left(\tanh \frac{\pi h}{a} - \tanh \frac{2\pi h}{a}\right) + \frac{k_o}{2a}\left(\coth \frac{3\pi h}{a}\right), \end{aligned}\right\} \tag{5}$$

where the subscripts $_i$ and $_o$ refer to the inner and outer pairs of rows in the symmetrical array. As in (3), capital letters refer to velocities of translation of the vortex centers.

By adding together the stream functions for the component vortex rows (2), with appropriate signs for the rotation in each case, and by displacing each row the required distances in the x and y directions (Fig. 2, upper panel), we obtain the stream function

$$\psi = \frac{k}{4\pi} \ln \left\{ \frac{\left[\cosh \frac{2\pi}{a}\left(y - \frac{3h}{2}\right) + \cos \frac{2\pi x}{a}\right]\left[\cosh \frac{2\pi}{a}\left(y + \frac{h}{2}\right) - \cos \frac{2\pi x}{a}\right]}{\left[\cosh \frac{2\pi}{a}\left(y - \frac{h}{2}\right) - \cos \frac{2\pi x}{a}\right]\left[\cosh \frac{2\pi}{a}\left(y + \frac{3h}{2}\right) + \cos \frac{2\pi x}{a}\right]} \right\}, \tag{6}$$

with streamlines as shown in Fig. 2.

The behavior of the single von Kármán vortex street can be compared with that of the compound vortex street in Fig. 7, which shows the relationships of (3) and (5) graphically for the case where $k = k_i = k_o$, with the dimensionless ratio aU/k as the ordinate plotted against the ratio h/a as the abscissa. In effect, the compound vortex street consists of two parts, the inner pair of vortex rows and the outer pair, each of which moves with its own velocity, U_i and U_o, $U_i = 0$ at $h/a = 0.24$ and is negative for lower values of h/a. That is, if $k_i = k_o$, the inner pair of rows is stationary when $h/a = 0.24$, moves in a direction opposite to that of the outer rows when the configuration of the array is very slender, and tends to move with the outer pair of rows when the array is broad (h/a large). U_o on the other hand is always positive, with a minimum value at $h/a = 0.23$. For the von Kármán vortex street, the relationship is much simpler; both rows move together, and the ratio aU/k increases monotonically with h/a without changing sign.

Both Fig. 7 and equations (5) show that, in general, the compound vortex street will not move as a unit, although it approaches this condition at large values of h/a. If, however, the ratio of k_i to k_o (the relative strengths of the inner and outer pairs of vortex rows) fulfills the condition

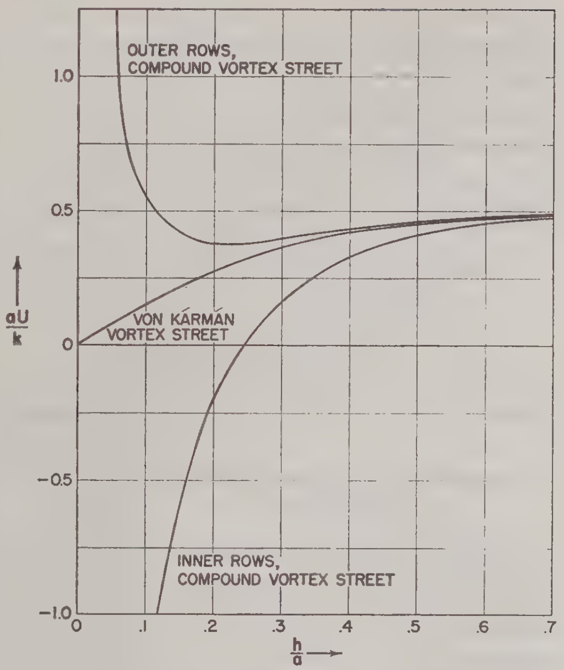

Figure 7. Velocities of translation of vortex rows of a von Kármán vortex street (middle line) and a symmetrical compound vortex street (upper and lower lines) as a function of geometry, for the case where the strengths of all vortex rows are equal. Velocity of translation (U) is plotted in dimensionless form as the ratio aU/k, where a is the wavelength and k is the strength of the vortices. Geometry of the arrays is plotted as the dimensionless ratio h/a, where h is the north-south interval between vortex rows and a is the east-west wavelength.

$$\frac{k_i}{k_o} = \frac{\tanh\dfrac{\pi h}{a} + \tanh\dfrac{2\pi h}{a} - \coth\dfrac{3\pi h}{a}}{\tanh\dfrac{\pi h}{a} - \tanh\dfrac{2\pi h}{a} + \coth\dfrac{\pi h}{a}}, \qquad (7)$$

which is derived by setting $U_i = U_o$ in (5), the array moves as a unit with respect to its system of coordinates.

Equation (6), as written, is valid only for the case where $k = k_i = k_o$. But, for the case where $U_i = U_o$, the equation must be modified by bringing k into the argument of the logarithm as an exponent. Each of the terms in brackets would thus be raised to the power k_i or k_o, depending upon whether it represented an inner row ($y = \pm h/2$) or an outer row ($y = \pm 3h/2$).

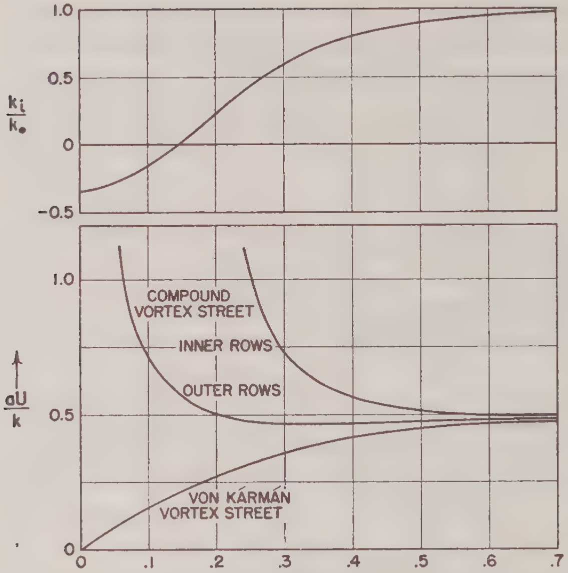

Figure 8.

Upper panel: Relationship between the strength of the inner vortex rows (k_i) and the outer vortex rows (k_o) of a compound vortex street for various geometries for the case where the array moves as a unit, with $U_i = U_o$.

Lower panel: Velocities of translation of vortex rows of a von Kármán vortex street (lower line) and a symmetrical compound vortex street (upper lines) as a function of geometry, for the case where the array moves as a unit, with $U_i = U_o$. The symbols are identified in the caption for Fig. 7.

Equation (7) is presented graphically in the upper panel of Fig. 8. Note that k_i/k_o diminishes from a value of 1.0 for large h/a to zero for $h/a = 0.145$, which implies that the strength of the central vortex rows diminishes with h/a and vanishes when h/a reaches 0.145.

The lower panel of Fig. 8 shows the behavior of the compound vortex street when it is constrained to move as a unit, with $U_i = U_o$. Fig. 8 can be compared with Fig. 7, where instead $k_i = k_o$. Note that, if a and U are held constant, the strength (k_o) of the outer pairs increases slightly as h/a decreases to about 0.34, then decreases (i.e., aU/k increases) for smaller values of h/a. The strength (k_i) of the inner vortex rows decreases continually as h/a decreases, reaching zero (aU/k goes to infinity) at $h/a = 0.145$. In contrast, the strength of the von Kármán vortex street increases continuously as h/a decreases, if a and U are held constant.

An important question, which will not be dealt with here, is that of the stability of the compound vortex street in response to perturbations. Domm (1954) performed stability calculations for a single von Kármán vortex street and showed that the range of conditions under which stability occurs tends to increase with time. It remains to be seen whether a perturbation analysis or the compound vortex street would yield analogous results.

Many refinements in the present theoretical analysis are possible by obvious extensions of the procedure used to obtain (5) and (6) from (1) and (2). For example, to obtain asymmetrical arrays, individual vortex rows could be displaced slightly to the east or west of the positions shown in Fig. 2. The existing fund of observations from the Kuroshio-Oyashio front, however, does not permit evaluation of the relative merits of such refinements. About all that can be expected is a semiquantitative evaluation to see whether the front bears any resemblance to a compound vortex street such as that shown in Fig. 2.

To permit comparison between theory and observation, the ratio aU/k was computed for three points in the array from (1). The points marked A and B in Fig. 2 (upper panel) lie on the axis of the array, midway between vortices of the inner row (A) and the outer row (B) ($x = 0, y = 0$ and $x = a/2, y = 0$, respectively). At these points the north-south component of velocity is zero, and the east-west component of velocity is given by

$$u(\mathrm{A}) = \frac{k_o}{a}\tanh\left(\frac{3\pi h}{2a}\right) - \frac{k_i}{a}\coth\left(\frac{\pi h}{2a}\right)$$

for point A, and by

$$u(\mathrm{B}) = \frac{k_o}{a}\coth\left(\frac{3\pi h}{2a}\right) - \frac{k_i}{a}\tanh\left(\frac{\pi h}{2a}\right)$$

for point B. Measurements (Table I) indicate that the ratio h/a has a value of approximately 0.42 for the Kuroshio-Oyashio region; by substituting this value into (7), we find that the ratio of strengths of the inner to the outer pair of vortex rows, k_i/k_o, must be very nearly 0.82 for the pattern to retain its geometry ($U_i = U_o$). Since $k_i = 0.82\,k_o$, for point A,

$$\frac{au(\mathrm{A})}{k_o} = \tanh\left(\frac{3\pi h}{2a}\right) - 0.82\coth\left(\frac{\pi h}{2a}\right) = -0.46, \tag{8}$$

and for point B,

$$\frac{au(\mathrm{B})}{k_o} = \coth\left(\frac{3\pi h}{2a}\right) - 0.82\tanh\left(\frac{\pi h}{2a}\right) = 0.56. \tag{9}$$

By applying a similar procedure to C (Fig. 2, upper panel), which lies at a midpoint between a vortex in an outer row and the neighboring vortex in an inner row ($x = 3a/4, y = h$), we have

$$\frac{au(\mathrm{C})}{k_o} = \frac{1}{2}\left(\tanh\frac{\pi h}{a} + \tanh\frac{5\pi h}{a} + 0.82\tanh\frac{\pi h}{a}\right) = 0.88; \tag{10}$$

v, which in this case is not zero, has a value given by

$$\frac{av(\mathrm{C})}{k_o} = \frac{1}{2}\left(\operatorname{sech}\frac{\pi h}{a} - \operatorname{sech}\frac{5\pi h}{a} + 0.82\operatorname{sech}\frac{\pi h}{a}\right) = 0.44; \tag{11}$$

then the resultant of the two components (10) and (11) is

$$\left(\left(\frac{au}{k_o}\right)^2 + \left(\frac{av}{k_o}\right)^2\right)^{\frac{1}{2}} = 0.98. \tag{12}$$

Thus the speeds at the three locations should occur in the proportions

$$A:B:C = -0.46:0.57:1.$$

Comparison of Theory With Observations. Table I shows the results of measurements made from the quarterly charts in the two volumes published by the Japanese Hydrographic Division, Maritime Safety Board. The values of h and a were estimated from 200-m temperature charts, and surface currents were estimated at points A, B, and C on the corresponding charts of GEK current measurements (see Fig. 2 for the locations of A, B, and C, and Fig. 3 for examples of these charts).

The values in Table I were obtained by locating, or attempting to locate, the major vortex centers that corresponded to those of the compound vortex-street model on each chart that provided sufficient coverage (usually those for the first and third quarters of each year). The value of a was then estimated by point-to-point measurement along the axis of the array to obtain the distance between successive vortices in the same row. Values for h were then estimated as distances between adjacent rows, measured perpendicular to the axis of the array. Values for velocity of surface currents were obtained by identifying midpoints between eddy centers on each temperature chart, and then looking for GEK measurements at, or very near, the same locations on the corresponding surface-current charts. Because of the distribution of observations, Table I represents conditions in the southern half of the front almost exclusively.

Once a compound vortex street was identified as such on any given chart, the procedure for taking measurements proved fairly straight-forward and unambiguous. However, the process of selecting individual eddies as "significant' and then relating them to each other as part of the model array was entirely subjective. In a number of examples the compound vortex street array, if present, was seriously distorted. A typical example appears in Fig. 3; the simplified model (middle panel) shows three pairs of central vortices, but a fourth pair can be tentatively identified in the easternmost portion of the upper panel, centered near 37°N, 154°E. This latter eddy pair has the same temperature structure as the third (easternmost) pair identified in the middle panel—slightly more than 9°C in the upper eddy and somewhat less than 6°C in the lower one—but the position of this fourth eddy pair is in no way consistent with the model. Most of such anomalies appeared on the charts in the easternmost portions of the Kuroshio-Oyashio front, and it is tempting to conclude that they represent stages in the downstream decay of the compound vortex street. On this premise, such anomalies were generally ignored, and none of the measurements in Table I was based upon them. It should be emphasized, however, that the values in Table I reflect choices based upon subjective judgment, and the numerical values must be regarded as only preliminary estimates.

Table I. Geometry and current velocity of the Kuroshio-Oyashio Front.

Year	Qtr.	Interval between rows (km)	Wave-length (km)	Ratio	Surface current (knots)			Relative speeds				
		h	a	$\bar{h}/\bar{a}$	A	B	C	$\bar{A}$	:	$\bar{B}$	:	$\bar{C}$
1956	4	150	–	–	−1.6	1.5	3.0					
		190			−1.1	1.9	2.5	−0.50	:	0.60	:	1.00
1957	4	150	370		−1.3	1.3	2.4	−0.54		0.54		1.00
		180		0.45								
1959	1	200	400		−1.1	0.8	2.3					
			350	0.53	−0.5		2.7	−0.32		0.32		1.00
	3	180	460	0.39	−1.1	–	3.5					
					−1.1		2.6	−0.36		–		1.00
1960	1	140	460		−1.4	1.5	2.1					
		180	380	0.38	−0.9		3.2	−0.43		0.54		1.00
	3	170	400		−1.1	1.3	2.4					
		150	350	0.43	−1.3		2.3	−0.50		0.54		1.00
1961	1	140	360	0.39	−1.7	1.0	2.6	−0.65		0.39		1.00
	3	150	440		−1.0	0.9	2.7					
		130	350	0.35	−1.2		2.9	−0.39		0.32		1.00
1962	1	180	390	0.46	−1.1	1.1	2.2					
							3.9	−0.37		0.37		1.00
	3	200	–	–	–	1.0	3.1	–		0.32		1.00
1963	1	140	440		−1.2	1.4	3.2					
		120	400	0.31	−0.7	1.6	3.4	−0.30		0.45		1.00
	4	210	430		−1.8	1.6	2.3					
		230	450	0.50	−1.3	1.1	3.0	−0.62		0.54		1.00
1964	1	–	400	–	−0.8	0.8	2.9					
					−1.1	1.5	2.7	−0.32		0.43		1.00
	3	200	450	0.44	−1.0	1.3	3.2	−0.31	:	0.41	:	1.00
Averages		170	404	0.42	−1.15	1.27	2.79	−0.43	:	0.44	:	1.00

Ratio of means $\bar{h}/\bar{a} = 170/404 = 0.42$. Relative mean speeds $\bar{A}:\bar{B}:\bar{C} = -0.41:0.46:1.00$.
Mean of ratios $\overline{h/a} = 0.42$. Mean of relative speeds $\overline{A:B:C} = -0.43:0.44:1.00$.
Theoretical relationship $A:B:C = -0.46:0.57:1.00$.

It is nevertheless noteworthy that the relative mean speeds at points A, B, and C in Table I are $A:B:C = -0.4:0.5:1$ as compared with the theoretical relationship $A:B:C = -0.46:0.57:1$. This agreement is better than one might expect from observations made with the GEK, selected on the basis of a rather simple model and grouped uncritically as simple averages.

Finally, equations (8), (9), and (12) can now be used to estimate k_o, since a and the velocities at points A, B, and C are known from Table I. The three independent estimates that result are:

$$\begin{aligned} k_o &= 5.2\times 10^9\ \text{cm}^2\ \text{sec}^{-1}, \text{ from the mean velocity at A,} \\ &= 4.8\times 10^9\ \text{cm}^2\ \text{sec}^{-1}, \text{ from the mean velocity at B,} \\ &= 4.9\times 10^9\ \text{cm}^2\ \text{sec}^{-1}, \text{ from the mean velocity at C.} \end{aligned}$$

Since the velocity at point B is based on fewer observations and is the most variable, the best estimate of k_o is probably 5.0×10^9 cm² sec⁻¹. The value of k_i is then 0.82 k_o, or 4.1×10^9 cm² sec⁻¹.

The parameters of the sea-surface model are now completely determined. The resulting characteristics are summarized in Table II.

Table II. Sea-surface characteristics of the compound vortex-street model of the Kuroshio-Oyashio Front.

Geometry: Wavelength, a = 404 km. Strength: Inner rows, $k_i = 4.1 \times 10^9$ cm² sec⁻¹.
N/S spacing, h = 170 km. Outer rows, $k_o = 5.0 \times 10^9$ cm² sec⁻¹.
Transport through array: 3.6×10^9 cm² sec⁻¹.
Velocity of array: 56 cm sec⁻¹ (48 km day⁻¹), toward the east.
Period of array: wavelength/velocity = 8.4 days.

The properties of the compound vortex-street model listed in Table II can be divided into two categories: (i) the geometry and strength, which are based upon observations interpreted in the light of theory, and (ii) the transport, array velocity, and array period, which are deduced from the theory and which in effect constitute predictions of properties that the Kuroshio-Oyashio front must have if it is in fact a compound vortex street.

The net transport through the model in Table II was computed as follows. Transport through any part of the array can be calculated from the difference in the stream function between any two points (outside of the immediate vicinity of the vortex centers). The net flow through the array is confined to the region of near-sinusoidal streamlines between the streamlines of value ±0.4 and 0 (Fig. 2). Outside this region are regions of closed flow surrounding the center of each vortex; the vortices in the central rows are enclosed by ellipsoids defined by streamlines of value 0, straddling the central axis, with one vortex center near each focus; the centers of vortices in the outer rows are each enclosed by a paraboloid, with the vortex center near its focus, the paraboloid in each case having a value of ±0.4. Thus the net transport through the compound vortex street is 0.8 k units or 3.6×10^9 cm² sec⁻¹ if k is taken to be 4.5×10^9 cm² sec⁻¹ (average of k_o and k_i, Table II). In more common units, the total flow through the model amounts to 3.6×10^5 m² sec⁻¹ (or m³ sec⁻¹ per meter depth). In Fig. 2, the flow between adjacent streamlines is 0.02 $k = 0.09 \times 10^9$ cm² sec⁻¹ (0.9×10^4 m² sec⁻¹).

A critical comparison of the two-dimensional model with its three-dimensional prototype would require extensive information on vertical changes in velocity within the Kuroshio-Oyashio front. Although this information is not now available, enough is known to provide an "order-of-magnitude" comparison.

Geostrophic transport in the Kuroshio and Oyashio combined is estimated to be approximately 50×10^6 m³ sec⁻¹ (Sverdrup et al. 1942, Uda 1964). A compound vortex street of strength $k = 4.5 \times 10^9$ cm^2 sec^{-1} (Table II) would transport the proper volume of water if it extended uniformly to a depth of 140 m. It would also transport the proper volume if the strength decreased exponentially so as to drop by half with each 75 to 80 m increase in depth, reaching values that are one-tenth those at the surface at depths of 250 to 265 m. If the use of GEK data results in an overestimate of k, or if geostrophic computations underestimate the total transport, the depth values calculated above would increase proportionately.

A velocity section across the Kuroshio and Oyashio presented by Koshlyakov (1961: fig. 2) shows that the geostrophic velocity in the vicinity of the Kuroshio-Oyashio front (35°N to 41°N, approximately) does in fact diminish rapidly with depth, from values of 25 cm sec^{-1} or more at the sea surface to one-tenth of that amount at depths of 300 to 900 m.

It is reasonable to conclude, therefore, that transport in the two-dimensional compound vortex-street model is of the proper order of magnitude. When more is learned about the transport in three dimensions in the Kuroshio-Oyashio front, it should be possible to extend the two-dimensional model to three dimensions by allowing k to diminish with depth in a realistic manner, as determined by observed decreases in current velocity with depth.

The significance of the speed and period of the theoretical compound vortex street (56 cm sec^{-1} and 8.4 days, respectively) remains to be considered. Observations suggest that the compound vortex-street array during most of the 1955–1964 decade was nearly stationary east of Japan, oscillating irregularly about an equilibrium configuration. Over longer periods of time it at least occurred with great frequency in one geographic location. Otherwise the compound vortex street would not appear on a whole series of quarterly charts (e.g., Fig. 3) and on a long-term average chart based on data taken between 1932 and 1960 (Fig. 5). These charts would appear very different if the vortex street progressed eastward by a distance of one wavelength every eight days.

We are thus left with some attractive conclusions and a set of dilemmas. The relatively simple concept of a compound vortex street accounts, in a manner that might be considered semiquantitative, for many of the major observed features of the complex Kuroshio-Oyashio front (including the distributions of temperature and density, the magnitude and direction of surface currents, and, to a degree, the volume transport). On the other hand, the kinematic theory implies that the compound vortex street should travel eastward whereas a variety of observations indicate that it tends to remain in one location. Worse still, the theoretical eastward velocity is proportional to k, the strength of the vortices, and it seems certain that k in the three-dimensional prototype must diminish with depth. We are led to the astonishing conclusion that the eastward velocity of the array must also diminish with depth.

A model that accounts for so much but fails in one particular is apt to be fundamentally correct but incomplete. The model deals with the kinematics of flow in the Kuroshio-Oyashio front and ignores the forces that govern that flow.

It seems pertinent to suggest that the eastward velocity of the model could produce a stationary array if the array's coordinate system were given an equivalent westward velocity by forces not considered in the simple theory of the model. Velocities of the proper magnitude and direction are produced by at least one class of phenomena: inertial planetary waves associated with changes in the Coriolis parameter with latitude (Moore 1963, for example) and a related class of planetary waves associated with changes in bottom topography on a rotating planet (Porter and Rattray 1964). This amounts to a suggestion that a search be made for solutions to the dynamic equations of motion having a form similar to that of equation (6).

Summary and Conclusions. At least two-thirds of the time during the 1955–1964 decade, the Kuroshio-Oyashio front east of Japan bore a marked resemblance to a symmetrical compound vortex street (Fig. 2), a type of flow consisting of two von Kármán vortex streets arranged side by side. The resemblance can be observed in quarterly charts of temperature at various depths, long-term average charts of the topography of isopycnal surfaces, quarterly charts of sea surface (GEK) currents, and, possibly, in charts of the dynamic topography of the sea surface. The wavelength was found to be about 400 km, the north-south interval between vortex rows, 170 km.

To permit quantitative comparisons, the kinematic theory first developed by von Kármán (1911) has been extended and generalized to include vortex streets of two or more rows of vortices. The theoretical model agrees well with the surface-current patterns in the Kuroshio-Oyashio front; currents at selected locations in both model and prototype flow in the same directions with the same relative speeds. Finally, if the two-dimensional model were extended to three dimensions by considering changes in current velocity with depth, volume transport of the proper order of magnitude could be obtained.

This marked resemblance between the unbounded nongeostrophic model and its prototype fails in one particular: the model predicts a substantial eastward translation of the vortex array whereas observations suggest that it remains more or less stationary. It is suggested that this contradiction might be resolved by a more complete analysis that would include the effects of Coriolis force and bottom topography.

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The Kuroshio-Oyashio Front: a System of Near-Stationary Vortices

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The author's kinematic model of the Kuroshio-Oyashio front, consisting of a pair of von Kármán vortex streets arranged side by side (or four parallel rows of Rankine vortices), accounted for many major features of that important region of the Pacific Ocean. However, the model did not include coriolis force; as a result, the model predicts an eastward displacement of the vortex system of about 50 cm sec^{-1}, whereas observations suggest that the vortices are more or less stationary. Recent theoretical work by Warren shows that, on a beta plane, circular currents of the type proposed in the vortex street model should be displaced westward at a rate which would, in large part, cancel the eastward velocity induced by other nearby vortices in the author's model without the beta plane effect. Taken together, these two theoretical analyses complement each other, providing a model which is complete and accounts for all major observed features of the Kuroshio-Oyashio front, at least to the degree which can be expected from first-order theory applied to the existing fund of published data. Some predictions based on the model are presented as a basis for field work designed to test the validity of the theoretical model.

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Collection of Juvenile Salmonids from Turbine Intake Gatewells of Major Dams in the Columbia River System

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Collection of Juvenile Salmonids from Turbine Intake Gatewells of Major Dams in the Columbia River System

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ABSTRACT

Turbine intake gatewells at Ice Harbor Dam on the Snake River were evaluated for their utility as collection areas of juvenile salmonids. The investigation took place from 1964 through 1966; results indicated that gatewell collecting is economical and efficient. One 3-man crew, in 1964, did the sampling; depending on water flow, the collections represented 2 to 6% of the total population. The sampling rate in the gatewells will enable a high degree of confidence to be placed on measurements of timing, migration rates, survival, and relative magnitude of the seaward migrations.

INTRODUCTION

The prohibitive cost of operating the collection equipment necessary to sample juvenile salmonids (*Oncorhynchus* spp.) in large rivers has restricted research on this phase of the life cycle. Also, high flows and associated debris during most of the downstream migration period often cause equipment, such as scoop traps, migrant dippers, and fyke nets, to become inoperative for extended periods. Some of these problems can be alleviated on rivers with hydroelectric dams by collecting juvenile salmonids from turbine intake gatewells which are usually an integral part of hydroelectric dams. Juvenile salmon and steelhead trout (*Salmo gairdnerii*) were found in gatewells by maintenance workers while they were removing debris. Long and Snyder[1] also found downstream migrants in gatewells at McNary and Bonneville Dams on the Columbia River.

This paper describes the equipment and technique used at Ice Harbor Dam on the Snake River, a major tributary to the Columbia. In 1964–66, the gatewells at the dam were fished to evaluate their utility as collection gear. Collections made in gatewells at other dams on the Columbia River in 1966 are mentioned briefly.

EQUIPMENT AND TECHNIQUES

Ice Harbor Dam has three Kaplan turbine units through which water flows at about 40,000 cubic feet per second, at a normal head of 93 feet. Each unit has three gatewells in which slots are provided to seal off the turbine from the forebay water during maintenance work. Gatewells of each unit are designated in Figure 1 as A, B, and C, starting from the south shore. Fish were collected from the area between the emergency and operating gate slots of all nine gatewells. A hydraulic cylinder prevented access to the entire gatewell area, but most of the water could be strained by a special sampling net 18½ by 11½ feet, which was about 6 feet deep when open (Figure 2). The net tapered slightly toward the center so that fish would slide into a 24-inch zippered bag. Rubberized cloth on the lower part of the bag protected the fish as the net was raised; enough water was retained to minimize loss of scales and crushing of the fish when large numbers were caught. The net frame was of tubular iron pipe and was hinged along the center so the net could be closed when being lowered into the gatewell. The frame was suspended from a harness ring by six lengths of ⅜-inch manila rope, and a pulley arrangement closed the net frame. Two sets of springs attached the frame to a spreader bar and permitted the net frame to open when the closing rope was released.

A crane lowered the closed net into the gatewell to the desired fishing depth. The net was then opened, slowly raised to the surface, and closed again to ease its withdrawal through the gate opening. To minimize mortalities from crushing, the fish were first netted from the surface waters of the gatewell and then from successively greater depths.

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[1] Clifford W. Long and George R. Snyder, Fishery Biologists, Fish-Passage Research Program, Bureau of Commercial Fisheries, U. S. Fish and Wildlife Service, Seattle, Washington. Unpublished.

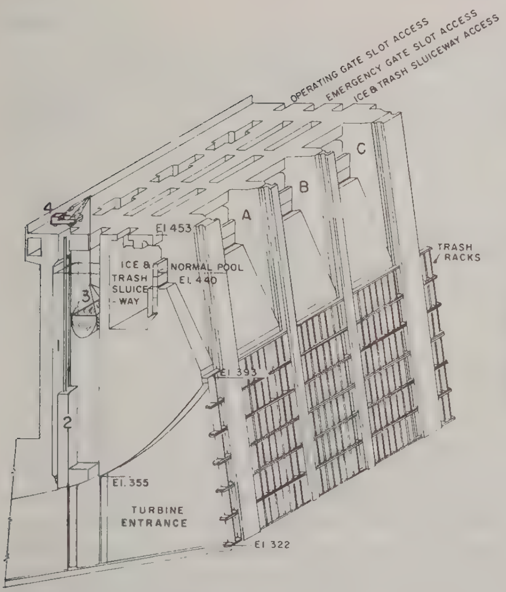

FIGURE 1.—Isometric view of one Kaplan unit of Ice Harbor Dam showing location and relative size of gatewells A, B, and C; elevations are feet above mean sea level. 1. Area unavailable for sampling. 2. Operating gate and cylinder in stored position. 3. Open gatewell net in fishing site. 4. Crane.

This procedure also gave us data on vertical distribution.

Fish were placed in a holding tank (2 × 2 × 6 feet long) in which aerated water was circulated. They were then transferred in groups of 15 to 20 from this tank to a smaller tank containing an anesthetic, Tricaine Methanesulphonate (MS-222). A 5% solution was made by dissolving 100 g of MS-222 in 2 liters of water. To maintain a 2-day supply of adequate strength, we placed the solution in an 11-oz beverage bottle wrapped with black tape and stored it in a dark, cool place to reduce exposure to light and heat. Dosage, which was measured by a 5- or 10-cc syringe and needle (the disposable type used in hospitals proved excellent), varied with species and water temperature, but was typically 2½ cc of solution per gal of water. This method of dispensing the anesthetic eased handling and ensured correct dosage. Some of the anesthetized fish were marked and the others were counted and examined for marks (see experiments described below). Fork lengths and scales were sampled weekly.

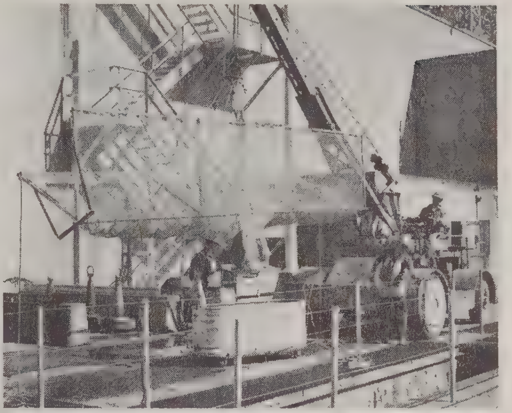

FIGURE 2.—Dip net in closed position above tank for receiving fish.

The utility of gatewells as collectors of juvenile migrants depends not only on the total number of fish collected, but also on the proportion of the total population sampled. The greater the sampling fraction, the greater the precision in estimates of population size, migration rates, timing, and survival. To estimate the proportion of the population sampled, about 25% of the fish collected in 1964 and 1966 were marked with a thermal brand (Groves and Novotny, 1965) and released upstream; the percentage recovery of marked fish in the gatewells of Ice Harbor Dam was the basis for the estimate.

The method assumed random mixing of marked with unmarked migrating fish. To test this assumption, marked fish were transported upstream in circulating, oxygenated water in a tank truck and released in the river at Fishhook Park (south shore) 8 miles above Ice Harbor Dam, and at Snake River Junction (north shore), 13 miles above the dam. Unmarked fish from gatewells were transported below the dam and released in the tailrace.

Marks that identified the fish released at the two sites were changed weekly to obtain a measure of mixing within the population of downstream migrants. We assumed that if proportionately equal numbers of marked fish were recaptured from each release site, mixing with the unmarked fish would be nearly complete.

TABLE 1.—*Numbers and percentages of marked chinook salmon released upstream and recovered at Ice Harbor Dam in 1964 and 1966*

Release group and year	Fishook Park (south bank) Total number		Percentage recovered	Snake River Junction (north bank) Total number		Percentage recovered
	Released	Recovered		Released	Recovered	
1964						
1	2,058	37	1.80	2,954	47	1.59
2	1,979	33	1.67	1,083	17	1.57
3	1,262	12	0.95	1,268	14	1.10
4	1,254	16	1.28	1,338	13	0.97
5	1,402	19	1.36	1,764	20	1.13
Total	7,955	117	1.47	8,407	111	1.32
1966						
1	1,854	41	2.21	1,860	46	2.47
2	1,655	14	0.85	1,727	22	1.27
3	1,328	12	0.90	1,353	20	1.48
4	1,030	17	1.65	724	9	1.24
5	690	14	1.42	1,025	19	1.85
Total	6,557	98	1.49	6,689	116	1.73

The proportion of the population sampled each year was based on catches in unit two, which was available for continuous sampling during all three years except for one week in 1964. Catches from unit one were substituted for that week. Maintenance or other fishing experiments made unit three in 1964 and units one and three in 1965 unavailable for sampling throughout most of the downstream runs. All three units were fished continuously only in 1966.

RECOVERIES OF FISH IN GATEWELLS

The combined totals for the chinook salmon (*O. tshawytscha*) and steelhead trout taken from unit two during the three years were 66,000 in 1964, 40,000 in 1965, and 105,000 in 1966. The estimated percentages of juvenile salmonids migrating down the Snake River that were strained from gatewells A, B, and C of unit two were 1.40% for chinook salmon and 1.75% for steelhead trout in 1964; 1.37 and 1.67% respectively in 1965; and 1.60% for chinook salmon in 1966 (when insufficient steelhead trout were marked and recaptured for a satisfactory estimate). Yearly estimates for the two species ranged between 0.90 and 2.50%, depending on water flow. Percentages were higher during low flows, when more of the river flow passed through the turbines, than during high flows, when most of the water passed over the spillway.

The degree of mixing of the marked fish released on different sides of the Snake River was examined in 1964 for both species and in 1966 for chinook salmon. Percentage recoveries for chinook salmon varied slightly each year among the five releases made at each site; in both years, however, the similarity in total recovery rates showed that marked fish released from each bank mixed consistently with the unmarked migrants (Table 1). The data suggested that gatewells A, B, and C of unit two at Ice Harbor Dam sampled about 1.5% of the chinook salmon migration under conditions of the experiment in 1964 and 1966. When gatewells of units one, two, and three were fished, as in 1966, the total proportion of the chinook salmon population sampled increased from 1.5 to about 4%, varying between 2% during high flows to as high as 6% during low flows.

Collections of juvenile salmonids from gatewells of other dams on the Columbia River in 1966 were: Priest Rapids Dam, 100,000; McNary Dam, 200,000; The Dalles Dam, 80,000; and Bonneville Dam, 100,000. The numbers of fish collected were comparable to those at Ice Harbor Dam, but estimates of the proportion of the total migrants passing each dam have been determined on the Columbia River only for Priest Rapids Dam (about 2% in 1965 and 1966). Further studies at these and other dams on the Columbia River will apply the same sampling techniques.

Many juvenile shad (*Alosa sapidissima*) were also captured each year in the gatewells at Bonneville Dam during October and November.

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A NEW SPECIES OF CARANGID FISH (*DECAPTERUS TABL*) FROM THE WESTERN ATLANTIC[1]

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ABSTRACT

A new species of *Decapterus* is described from off the coast of Colombia, Venezuela and Florida. It is differentiated from the two other western Atlantic species of *Decapterus* by the numbers of scales in the curved lateral line, scutes in the straight lateral line, and total scales and scutes (61–78 scales, 34–48 scutes, 103–119 total in the new species; 37–56 scales, 32–46 scutes, 77–98 total in *D. punctatus*; 68–79 scales, 23–32 scutes, 119–133 total in *D. macarellus*).

INTRODUCTION

The carangid genus *Decapterus* occurs in most tropical and subtropical marine waters of the world. Several of the species, at least, occur in large pelagic schools. These are generally found in inshore waters, although the schools of young, especially, may occur in oceanic areas. Some species are utilized for human food, and some species are caught for live or processed bait for other fishes.

My recent studies, based upon a large amount of recently collected material, as well as specimens preserved in a number of museums, indicate that the species composition of *Decapterus* is inadequately known and even the morphological limits of the genus need critical study. The genus *Decapterus* was established by

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[1] Contribution No. 78, Tropical Atlantic Biological Laboratory.

Contributions in Marine Science, Vol. 13, 1968

Bleeker in 1851 with the type species *Caranx kurra* Cuvier, 1833. Species of the genus were dealt with by Nichols (1911, 1936, 1951). Eastern Atlantic species were considered by Norman (1935), Trewavas (1945), Blanc and Bauchot (1961) and Cadenat and Marchal (1963). Western Atlantic species were described by Ginsburg (1952). The most recent review of the entire genus, by Bertin and Dollfus (1948), is in need of revision.

Recent literature (Ginsburg 1952; Briggs 1958; Berry in McClane 1965) has defined only two species of *Decapterus* from the western Atlantic—*Decapterus punctatus* (Agassiz in Spix 1829) and *Decapterus macarellus* (Cuvier in Cuvier and Valenciennes 1833). The names of these two species have been considered, recently (Blanc and Bauchot 1961; Cadenat and Marchal 1963), to apply to species in the eastern Atlantic. A third species from the eastern Atlantic, with a confusing nomenclatorial history, has been referred to by the name of *Decapterus sanctaehelenae* (Cuvier in Cuvier and Valenciennes 1833) by Cadenat and Marchal (1963); and in their check list, Jordan, Evermann and Clark (1930) used that name to apply to a supposed third species from the western Atlantic. My current review of this genus in the western Atlantic is benefited from a large and significant amount of specimen material collected in the last few years by the research vessels OREGON, COMBAT, SILVER BAY, CALAMAR and by James K. Dooley. This has been supplemented with recent collections from the eastern Atlantic by the LA RAFELLE and THIERRY of the Guinean Trawling Survey and the UNDAUNTED, GERONIMO and PILLSBURY. These studies have produced the following conclusions:

1) Three species of *Decapterus* occur in the western Atlantic, *D. punctatus*, *D. macarellus*, and a new species described herein.
2) Cognate (or geminate) forms, or species of these, occur in the eastern Atlantic.
3) The scientific name of the eastern Atlantic cognate species of *D. punctatus* is *D. sanctaehelenae* (Cuvier in Cuvier and Valenciennes 1833).
4) *D. macarellus* occurs on both sides of the Atlantic.
5) The new species described here from western Atlantic material also occurs at St. Helena in the eastern Atlantic.
6) Four species of *Decapterus* occur at St. Helena, and one of these (the "stonebrass") apparently lacks a valid scientific name.
7) *Caranx rhonchus* Geoffrey St. Hilaire, 1809, has recently been placed in the genus *Caranx*, but is a valid species of *Decapterus*.
8) Indo-Pacific species of *Decapterus* are in need of revision, and although they appear to be specifically distinct from Atlantic species, at least one may represent a circumtropical species complex (including *D. macarellus*).

CHARACTERS AND METHODS

The methods of taking accurate data are frequently dependent on knowledge of morphology and ontogeny of the characters, and the 2 topics are combined here. This section relates primarily to the 3 western Atlantic species of *Decapterus*, but the several *Decapterus* species I have examined from other areas con-form to these characters and methods, and for most of them, so do species of *Selar*, *Trachurus*, and other Caranginae. Only western Atlantic specimens (excluding Bermuda) are used in the species diagnoses and in the tables (except for 2 St. Helena specimens in Table 5).

Dorsal fin. The dorsal fin is continuous in small specimens; the membrane connecting the 8th and 9th dorsal spines exists to a size of *ca.* 30–50 mm SL. The first dorsal fin normally has 8 spines (one aberrant specimen had only 4); the third spine is normally the longest, and the longest spine is *ca.* 10–40% longer than the longest softray. The second dorsal fin has one anterior spine (that is *ca.* one-half as long as the longest softray) and 29–37 branched softrays; the first softray is normally the longest and *ca.* 10–28% longer than the longest anal fin softray; the terminal finlet in *punctatus* is close to the penultimate softray in small specimens (*ca.* less than 18 mm SL), and becomes displaced posteriorly at larger sizes; the membrane connecting the finlet to the penultimate softray degenerates at *ca.* 45–50 mm SL.

Anal fin. The anal fin is continuous in small specimens; the membrane connecting the second and third spines exists to *ca.* 30–40 mm SL. The first anal fin has 2 spines, with the first the slenderer but usually *ca.* 3–12% longer than the second. The second anal fin has one anterior spine (*ca.* one-half as long as the longest softray) and 24–31 branched softrays; the first softray is normally the longest; ontogeny of the finlet is similar to that in the dorsal fin.

Lengths of dorsal and anal rays. Spines and softrays measured from anterior point of insertion to tip of ray.

Pectoral fin. Each pectoral fin has one spine on its dorsal margin (*ca.* one-fifth to one-third as long as the longest softray) and 18–23 softrays; the first softray is unbranched, the others branched; the fourth softray is the longest, with the third only slightly shorter. Bilateral variation occurs in the number of softrays (27% of the sample of *tabl* had one more softray on one side than the other, 20% of *punctatus*, and 8% of *macarellus*), but the variation is random, either right or left sides having the extra ray. The pectoral fin is *ca.* 45–80% longer than the pelvic fin.

Pelvic fin. Each pelvic fin has one lateral spine (*ca.* one-half to two-thirds as long as the longest softray) and 5 branched softrays (one abnormal specimen had only 4 softrays in the right fin); the second softray is the longest with the first only slightly shorter.

Lengths of pectoral and pelvic fins. Measured from the dorsal (pectoral) or lateral (pelvic) point of insertion of the spine to the tip of the longest ray.

Caudal fin. In *Decapterus*, as in all Carangidae, there are 9 dorsal (superior) and 8 ventral (inferior) principal caudal fin rays, with the most dorsal and the most ventral ray unbranched and the others branched; there are *ca.* 8–9 secondary caudal rays in both the dorsal and ventral lobes. The caudal fin rays are all considered to be softrays, even though the 3–4 most anterior dorsal and ventral secondary rays are not segmented. The most ventral of the dorsal principal rays is usually the shortest ray in the fin; the longest ray in the dorsal lobe is the third from the top principal ray, and the corresponding ray in the ventral lobe is its longest; the dorsal and ventral lobes are of similar length.

Gillrakers. Gillrakers occur on both the lateral and medial sides of arches 1–4 (numbered from lateral to medial); gillrakers on the lateral side of the first arch are about 3–8 times as long and almost twice as numerous as on the medial side of the first arch; the gillrakers on faces of the other arches generally decrease slightly in number (toward the fourth arch), with the medial side of the fourth arch lacking upper limb gillrakers and having the lowest count.

The count of gillrakers on the lateral side of the first arch is used in the text, in characterizing the species. The gillraker at the angle of the upper and lower limb has the major portion of its base over the ceratobranchial bone and is included in the count of the lower limb. Occasionally, rudimentary gillrakers (with the base width of the raker equal to or greater than its length) occur at the anterior ends of the limbs, over the epibranchial and hypobranchial bones, and these are included in the counts for each limb. The number of gillrakers over the hypobranchial has a slight positive correlation with that over the ceratobranchial. Apparently, gillrakers continue to form on the anterior ends of the upper and lower limbs to a size of *ca.* 55 mm SL; specimens smaller than 60 mm SL were not included in the tables of frequency distributions for the 3 species.

A slight bilateral variation exists in gillraker numbers, that is randomly right or left. Counts were usually made only on the right side of each fish. It is often necessary to slightly damage the opercular and isthmal attachments and to use compressed air to adequately expose all of the gillrakers for counting.

Branchiostegal rays. Branchiostegal rays were 3 + 4 on both sides in all specimens counted (22 specimens of *tabl*, 18 of *punctatus*, and 10 of *macarellus*).

Vertebrae. Number of vertebral centra is intraspecifically very constant in all Carangidae. I have examined all genera and many species (some in appreciable quantity) of the family and find no variation in number within a species, with four exceptions: 1) One 106-mm specimen of *Decapterus sanctaehelenae* from St. Helena (ZMK uncataloged) has 10 + 14 centra, and 52 other specimens of the species have 10 + 15. 2) One *Oligoplites saurus inornatus* has 10 + 17 centra, and 19 others have 10 + 16. 3) One *Hemicaranx amblyrhynchus* has 10 + 15 centra with a deformity of the last centrum, and 15 others have 10 + 16. 4) The *Caranx sexfasciatus* species complex varies between 10 + 14 and 10 + 15 dependent on geographic area of occurrence. Although Bertin and Dollfus (1948:6) did not consider vertebral number to be of value in specific differentiation of *Decapterus*, my data show (with the one exception given above) that *tabl* and *macarellus* have 10 + 14 centra and *punctatus* and *sanctaehelenae* have 10 + 15.

Trunk vertebrae in *Decapterus* have a bilateral pair of pleural ribs on centra 3–10. Caudal vertebrae counts include the urostyle as the terminal centrum; the posterior surface of the first interhemal spine ankyloses to the anterior surface of the first hemal spine at a small size.

Scales. Body scales are cycloid with concentric circuli around the focus, and usually have one or two scallops on the anterior margin with two or three weak radii separating these and extending from the anterior margin to the focus. The body is covered with scales except for small areas in the axil of the pectoral fins and beneath each pelvic fin. Scales extend anteriorly on top of the head to above the anterior part of the eye and largely cover the interorbital area; they extend ventrally over most of the opercle, subopercle and interopercle; and from the anterior part of the preopercle scales extend onto the cheek to the end of the maxilla. The spinous dorsal and spinous anal fins are scaleless. Rows of scales occur on the membranes between the first three of four rays of the soft dorsal and soft anal fins. Rows of scales occur along the anterior margins of the softrays of the pectoral and pelvic fins and on the membranes between the rays of the caudal fin. There are no bilateral, paired caudal keels. The scaled sheath along the bases of the dorsal and anal fins is low. The posterodorsal accessory lateral line (supratemporal commissure) is relatively short, converging and ending on each side near the posterior end of the supraoccipital crest.

Lateral line. The lateral line in *Decapterus* and all Caranginae consists of an anterior curved (dorsally arched) part, that is marked by a single row of pored scales beginning at the cleithrum, and a posterior straight (horizontal) part, that has a single row of pored scales and scutes and ends on the median portion of the caudal fin. The "junction" of the curved and straight parts is defined as the point where (extending posteriorly) the lateral line ceases to bend and becomes straight and generally aligned with the horizontal body axis. It is not a precise point, and a somewhat arbitrary point must be selected in measuring and counting. The site of this junction varies within a species and frequently varies on each side of a fish, but when the degree of intraspecific variation is known, it can be a useful taxonomic character. A scute in carangids is defined as a modified pored lateral-line scale that is enlarged (compared to other body scales), usually thickened, and has its posterior margin terminating either in a pointed spine or an apex, with the angle of the scute formed by this margin being about 110° or less.

The total number of scales and scutes in the lateral line appears to be present in the smallest specimen counted for each species (*punctatus*, 29 mm; *tabl*, 65 mm; *macarellus*, 37 mm). The differentiation of scales to scutes is not complete at the smallest sizes in *punctatus* and *macarellus*, however. In *punctatus*, scutes tend to form into the posterior part of the straight lateral line until a size of about 48 mm, although this may be completed in some specimens as small as 30 mm. In *macarellus*, straight lateral-line scutes are apparently all formed in specimens 51 mm and larger, but not in 6 specimens of 37 to 50.5 mm. Data on these smaller specimens of *punctatus* and *macarellus* were not included in Table 4.

Lengths of curved and straight parts of lateral line. The curved lateral line was measured as a chord of its arc; the straight lateral line was measured from the junction to the end of the last scale over the caudal fin.

Ratio of lateral line. The lateral-line ratio is the quotient of the length of the straight part divided by that of the curved part.

Dentition. Bertin and Dollfus (1948:6) minimized the value of dentition in *Decapterus* taxonomy, while based on data of Suzuki (1962:215–216), differences in tooth patterns will differentiate six nominal species of *Decapterus* he identified from Japan. The dentition of the specimens of *tabl* is generally similar in pattern, but quite variable in number and extent—suggesting that both ontogenetic changes and intraspecific variation should be analyzed in describing dentition in other *Decapterus* species. Also, teeth are easily broken off, especially in the jaws, during laboratory examination. They are present in most specimens of the three western Atlantic species in both jaws, on the tongue and palatines, and laterally on the head and medially on the shaft of the vomer.

Body measurements. Standard length (SL)—tip of snout to end of caudal base (hypural bones) along horizontal body axis. Fork length (FL)—tip of snout to end of shortest median principal caudal fin ray. Total length (TL)—tip of snout, through horizontal body axis, to a vertical of tip of longest caudal fin ray. Head length—tip of snout to posterior margin of fleshy opercle. Eye diameter—horizontal diameter of orbit (often estimated and difficult to determine due to thickness of adipose eyelid). Postorbital head length—posterior margin of orbit to posterior margin of fleshy opercle. Upper jaw length—tip of snout to posterior margin of maxillary. Maxillary depth—greatest depth from dorsal margin of supramaxilla to ventral margin of maxilla. Body depth D1 to P2—origin of first dorsal fin to insertion of pelvic fin in saggital plane, the measurement inclined anteroventrally. Body depth D2 to A1—origin of second dorsal fin to origin of first spine of anal fin, the measurement inclined posteroventrally. Body depth maximum vertical—measured in saggital section, usually occurring around insertion of spines 4–7 of first dorsal fin.

KEY TO WESTERN ATLANTIC *DECAPTERUS*

1A. Dark spots (10–14) present along curved lateral line (at sizes larger than *ca.* 90 mm SL). Curved lateral line strongly arched (Fig. 4). Curved lateral line with 37–56 scales and usually 1–5 scutes. Total lateral line scales and scutes (excluding peduncle scales) 72–98. Vertebrae 10 + 15 .... *Decapterus punctatus* (Fig. 2).

1B. No spots in curved lateral line. Curved lateral line moderately to weakly arched (Figs. 5 and 6). Scales in curved lateral line 61 or more. No scutes in curved lateral line. Total lateral line scales and scutes 103 or greater. Vertebrae 10 + 14 .... 2.

2A. Curved lateral line moderately arched (Fig. 5). Anterior scales in straight lateral line 0–8. Scutes in straight lateral line 34–44 .... *Decapterus tabl* (Fig. 1).

2B. Curved lateral line weakly arched (Fig. 6). Anterior scales in straight lateral line 19–33. Scutes in straight lateral line 23–32 .... *Decapterus macarellus* (Fig. 3).

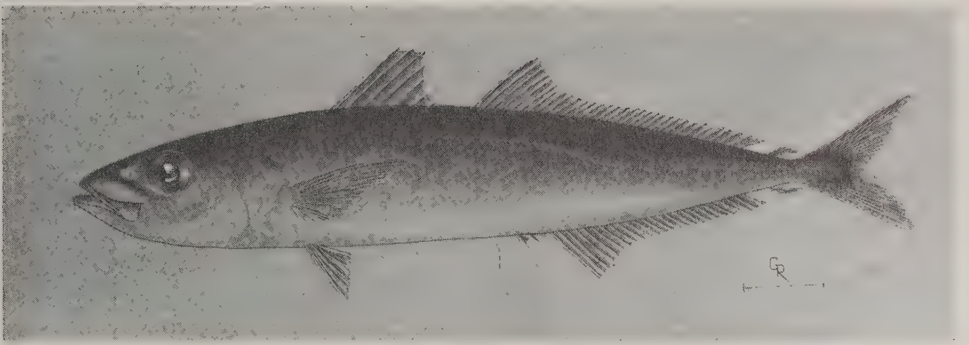

FIG. 1. *Decapterus tabl,* TABL 101476, 182 mm SL, OREGON station 4843, caught off Colombia, in a trawl fishing on bottom at 100 to 120 fathoms.

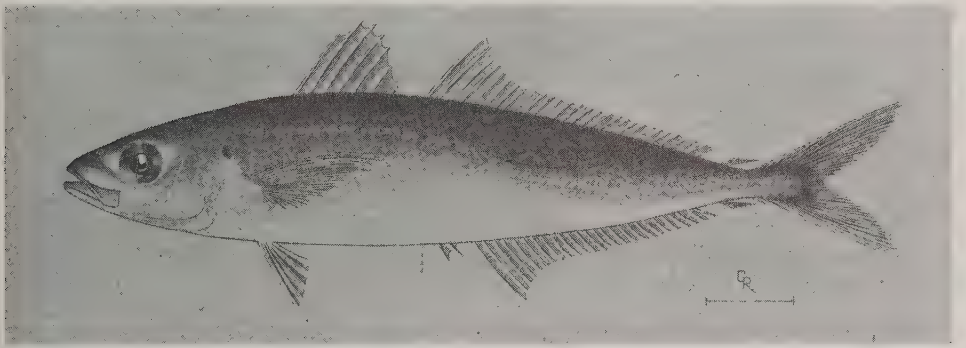

FIG. 2. *Decapterus punctatus,* TABL 101477, 159 mm SL, SILVER BAY station 5737, caught off North Carolina, in a trawl fishing on bottom at 25 to 29 fathoms.

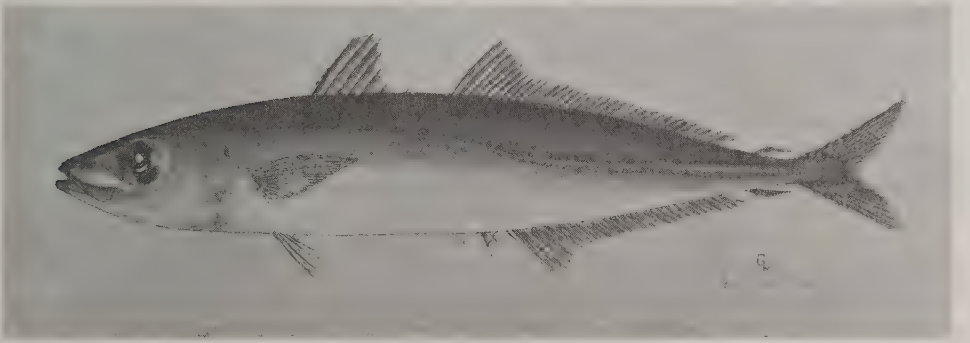

FIG. 3. *Decapterus macarellus,* USNM 84030, 172 mm SL, Woods Hole, Massachusetts.

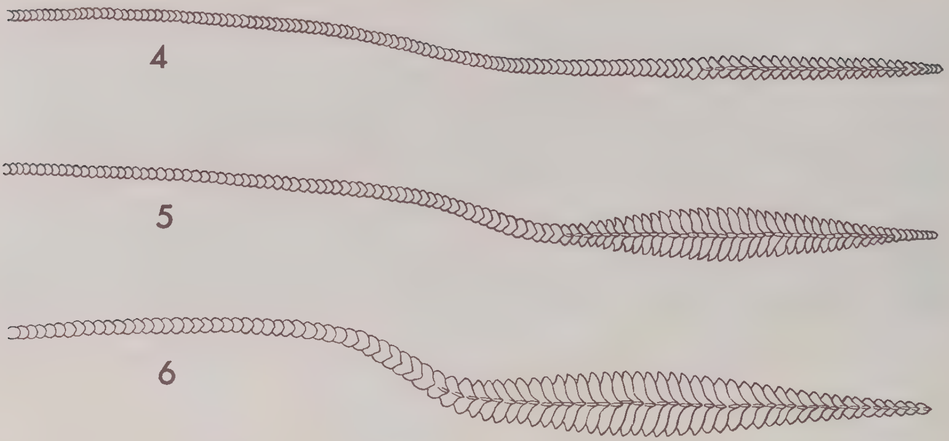

Fig. 4. *Decapterus macarellus.* Fig. 5. *Decapterus tabl.* Fig. 6. *Decapterus punctatus.* Contour of the lateral lines and relative size of their scales and scutes for the specimens of Figs. 1–3.

DECAPTERUS TABL, NEW SPECIES

REDTAIL SCAD

FIG. 1

Decapterus punctatus (*non* Cuvier): Ginsburg, 1952: 87 (in part; "the New Smyrna variant"). Berry in Anderson and Gehringer 1959: 64 (part of stomach contents of *Coryphaena hippurus*).

Diagnosis. A *Decapterus* with a relatively long curved lateral line, of 61–78 scales; no spots or scutes in curved lateral line and usually 0–8 scales in anterior part of straight lateral line; 34–48 scutes; lateral-line scales and scutes (excluding peduncle scales) 103–119; gillrakers 10–12 + 30–33; pectoral softrays 20–22; vertebrae 10 + 14.

Description. Frequency distributions of correlated dorsal and anal fin softray counts are given in Table 1. The dorsal and anal rays are positively correlated, with modal values of D. 31–32 and A. 25. Frequency distributions of correlated

Table 1

Frequency distribution correlation for dorsal and anal softrays in 50 specimens of *Decapterus tabl.*

		DORSAL					
		29	30	31	32	33	34
ANAL	27	..	..	..	..	2	2
	26	..	..	3	4	7	3
	25	1	1	10	11	2	..
	24		3	.	1	..	.

TABLE 2

Frequency distribution correlation for upper and lower limb gillrakers in 47 specimens of *Decapterus tabl.*

		LOWER			
		30	31	32	33
UPPER	12		4	4	2
	11	1	7	16	2
	10	1	6	4	

numbers of upper and lower limb gillrakers on the lateral side of the first arch are given in Table 2. The upper and lower limb gillrakers are positively correlated, with a mode at 11 + 32. Frequency distributions of dorsal, anal, and pectoral softrays and of gillrakers are shown in Table 3 for comparison with the other two western Atlantic species. Gillrakers apparently had not completed formation in the smallest specimen (65 mm), and its count (9 + 30) is not included in Tables 2 and 3. Gillrakers over the hypobranchial range 9–11. One rudimentary gillraker was present at the anterior end of the upper limb of almost half of the specimens, and two rudiments were present in one specimen. Rudiments were lacking on the anterior end of the lower limb in more than two-thirds of the specimens; the others had one rudiment. The shape of the lateral line is illustrated in Figure 5. Frequency distributions of scales and scutes in various parts of the lateral line are given in Table 4. Scales in the curved and anterior parts of the lateral line (anterior to the first scute) range 65–78, mean 71.4. Posterior scales in the straight lateral line (on the peduncle and caudal fin, following the terminal scute) range 4–8, mean 6.0. Total scales in the lateral line (including the peduncle scales) range 110–124, mean 116.7. Vertebrae are consistently 10 + 14 in the holotype, 48 paratypes, and the three other specimens examined.

Ranges for significant morphometric characters of the larger specimens are given in Table 5, where paratypes of 156–199 mm SL from five collections are distinguished from the 14 larger paratypes of 195–219 mm from OREGON sta. 5711 and the two very large specimens from St. Helena. The larger paratypes, compared to the smaller ones, evidence a longer head, larger eye, longer pectoral and pelvic fins, and longer third spine and first softray in the dorsal fin. I presume these differences represent an allometric growth pattern in these characters. The St. Helena specimens are generally similar to *tabl* from the western Atlantic in body proportions.

The junction of the curved and straight parts of the lateral line is usually under the 13th to the 16th dorsal softray. The point of junction has a slight bilateral variation in most specimens, but the curved portion is up to 10% longer on one side than the other in a few specimens.

Dentition. All teeth small, short, conical, granular or deciduous, some slightly recurved. Teeth usually present in both jaws and on vomer, palatines, and tongue, but variable between otherwise similar specimens and with ontogeny. Upper jaw teeth in a short, irregular row near symphysis; lower jaw teeth in

TABLE 3

Frequency distributions of numbers of softrays in the dorsal, anal, and pectoral fins and of gillrakers in the three western Atlantic species of *Decapterus*

DORSAL SOFTRAYS

	29	30	31	32	33	34	35	36	37	x̄	n
punctatus	2	8	18	29	12	5	..	..	..	31.8	74
tabl	1	4	14	16	11	5	..	..	..	31.9	51
macarellus	..	..	1	1	14	9	9	2	2	34.0	38

ANAL SOFTRAYS

	24	25	26	27	28	29	30	31	x̄	n
punctatus		1	7	30	28	6	2	..	27.5	74
tabl	4	26	17	4	..	..	..	..	25.4	51
macarellus	..	..	..	2	9	18	7	2	28.9	38

PECTORAL SOFTRAYS (bilateral counts)

	18	18	19	19	20	20	21	21	22	22	23		
	18	19	19	20	20	21	21	22	22	23	23	x̄	n
punctatus	13	10	35	4	7	..	..	..	..	..	..	18.9	69
tabl	..	..	..	..	4	8	32	6	1	..	..	20.9	51
macarellus	..	..	..	..	..	..	12	2	19	1	2	21.7	36

GILLRAKERS: UPPER LIMB

	9	10	11	12	13	14	15	16	x̄	n
punctatus	..	..	5	13	61	49	12	2	13.4	142
tabl	.	11	26	10	.	.		.	11.0	47
macarellus	1	4	18	12	1	..	..	..	11.2	36

GILLRAKERS: LOWER LIMB

	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	x̄	n
punctatus	..	..	1	..	9	21	41	25	22	14	5	2	1	..	1	36.8	142
tabl	2	17	24	4	..	..	..	..	..	..	..	..	..	..	..	31.6	47
macarellus	..	..	1	1	1	3	6	5	9	10	..	..	..	..	..	37.1	36

a single row along most of jaw; teeth in both jaws decreasing in extent with growth. Palatine teeth only on anterior head of bone, variable in extent and number. Vomerine teeth present laterally as a patch on head of vomer and medially in a single row or narrow band on shaft of vomer; the teeth very variable in number and extent of coverage in specimens of similar size, but generally increasing in both with growth, as is shown by the following selected examples comparing number of teeth with body length:

standard length	head of vomer	shaft of vomer
65	10	3
73	14	5
165	16	8
183	24	5
184	4	1
201	56	29
213	54	19
217	24	4
351	60	36
360	160	38.

Tongue teeth usually in a narrow band, slightly broader posteriorly, or a single row in some specimens; the band or row mainly on posterior part of tongue, and generally but variably decreasing in number of teeth and size of band with growth; no teeth on tongue of the 360 mm specimen from St. Helena, but a short, distinct band present in the 351 mm specimen.

Pigmentation. Adults originally preserved in 10–15% formalin and maintained in 40% isopropanol. Dorsal part of snout and head and dorsal third to half of body dark, the dark on head extending down slightly onto operculum and preoperculum; a dark opercular spot; tips of jaws, isthmus, branchiostegal membranes, and inner surface of operculum dusky; inner surface of lower jaw and dorsal surface of tongue dark to dusky. Dark pigment on dorsal part of body extending into a dark oval area over fleshy part of caudal peduncle and fin, this area encompassing the terminal scutes and scales of lateral line; ventral part of body clear. Rays of spinous and soft dorsal fins dusky, rays of other fins less dusky, especially pelvic fin rays; interradial membranes mostly clear. Peritoneum clear.

Coloration. Kodachrome slide (35 mm) of a freshly caught specimen from OREGON station 4843: Top of head dark, grading into metallic blue along back and upper part of body, this blue on body changing into dusky silver about one-half way down body with a silvery or white belly; most of straight part of lateral line bright silver, especially scutes; most of head silvery with dorsal part of snout very dark and upper jaw dusky. First dorsal fin with spines dark, membranes clear. Second dorsal fin with membranes clear, rays dark with tips of anterior 10 or so rays and the finlet tinged with red. Caudal fin bright red. Anal fin clear. Pectoral fin slightly dusky on dorsal part. Pelvic fins apparently tinged with red.

Size. The largest specimen examined (BMNH 1910.9.9.18) is from St. Helena, 360 mm SL, *ca.* 410 mm or 16.1 in. TL, and weighs 558 gms. (1.2 lbs.). The largest specimen examined from the western Atlantic (TABL 103024), 219 mm SL, *ca.* 332 mm or 13.1 in. TL, weighs 115 gms. (0.25 lb.).

Distribution. Currently known only from 55 specimens of 11 collections—from off North Carolina, off the east coast of southern Florida, off Colombia, off

TABLE 4

Frequency distributions of numbers of scales and scutes in the lateral line for the three western Atlantic species of *Decapterus*.

CURVED LATERAL LINE: SCALES

	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	x̄	n
punctatus	1	1	2	5	6	20	16	15	13	22	18	26	10	8	6	13	9	7	8	2																								46.9	208
tabl																									1	1	1	2	4	9	3	7	7	4	6	2	2	1				1		68.0	50
macarellus																																1	3	7	2	3	5	2	2	3	1		3	72.9	33

CURVED LATERAL LINE: SCUTES

	0	1	2	3	4	5	6	x̄	n
punctatus	10	24	50	69	38	13	1	2.7	205
tabl	51							0.0	51
macarellus	39							0.0	39

STRAIGHT LATERAL LINE: ANTERIOR SCALES

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	x̄	n
punctatus	205	2	1																																0.0	208
tabl	8	4	9	3	9	8	7		2																										3.2	49
macarellus																				1	2	1	2	5	2	1	3		4	8	3	1	1	1	26.3	35

STRAIGHT LATERAL LINE: SCUTES

	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	x̄	n
punctatus										1	2	6	14	17	33	42	38	30	14	2	5			1			38.2	205
tabl												3	1	5	4	6	7	13	3	3	3	2				1	39.2	51
macarellus	1	1	1	6	8	3	4	7	3	1																	28.0	35

TOTAL LATERAL LINE (excluding peduncle scales)

	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105
punctatus	2			4	8	6	5	11	20	19	21	20	17	13	12	21	11	7	4	4	2	1							
tabl																											1		1
macarellus																													

	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	x̄	n
punctatus																													88.1	208
tabl	2	5	5	5	7	5	5	7	1	2	1	1	1	1															110.6	50
macarellus														1		2		2		4	6	2	2	4	4	1	1	1	126.8	30

Table 5

Body proportions (in percent of standard length) of the three western Atlantic species of *Decapterus* including two specimens of *D. tabl* from St. Helena (315–360 mm SL)

	tabl			*punctatus*	*macarellus*
Standard length (mm)	156–199	195–219	351–360	140–183	145–256
Total length	113–115	115–115	114	116–117	115–115
Fork length	104–106	106–107	106	106–108	106–107
Head length	27.5–29.0	29.5–31.2	28.8–30.0	25.5–27.5	25.2–26.8
Eye diameter	6.5–7.4	7.1–8.4	7.1–8.5	7.1–7.9	5.9–6.9
Snout length	8.3–10.4	9.7–11.0	9.4–10.7	7.3–9.1	8.3–9.4
Postorbital head	11.8–13.0	11.2–12.9	11.4–11.9	10.2–12.3	10.5–11.4
Upper jaw	9.2–9.9	9.8–10.1	10.0–10.3	8.3–8.6	7.8–8.5
Maxillary depth	2.8–3.4	3.1–3.5	3.1–3.2	2.9–3.2	2.7–3.1
Depth D1 to D2	17.0–20.2	17.4–20.9	20.1–20.2	18.8–22.0	17.4–19.2
Depth D2 to A1	16.5–20.0	17.2–19.1	19.8–20.0	19.5–23.1	17.3–18.9
Depth max. vert.	16.7–19.8	17.4–19.4	19.5–19.7	18.8–23.0	16.1–18.9
Pectoral length	16.4–18.1	19.8–22.2	18.8–19.4	18.2–23.5	15.3–17.5
Pelvic length	10.5–12.1	11.9–12.9	11.4–12.9	11.0–13.0	9.9–12.1
D. spine (longest)	12.4–13.9	12.6–15.0	13.2–13.8	12.4–15.6	10.3–13.6
D. softray (longest)	10.2–11.2	11.3–12.8	10.9–11.4	11.5–12.4	8.9–9.5
A. spine (longest)	2.9–3.7	2.8–3.4	2.9–2.9	4.2–4.6	3.2–3.8
A. softray (longest)	8.8–9.5	8.8–10.2	9.5–9.9	10.1–11.3	7.5–8.7
Lateral-line ratio	0.61–0.91	0.68–0.98	0.67–0.81	0.92–1.16	0.79–1.05

Venezuela, and from St. Helena. The two smallest specimens (65–73 mm) were taken at the surface; the larger specimens from Florida (117 mm) and Colombia (149–219 mm) were taken in nets fishing on the bottom at 75 to 120 fathoms; the specimen from off Venezuela (194 mm) was taken in a bottom net fishing at 220 fathoms. Although the specimens taken in bottom-fishing nets may have been taken while the nets were descending or ascending, these records indicate that in its adult stage this a more offshore and deeper living species than *punctatus* or *macarellus*.

Holotype: USNM 202744, 202 mm SL, OREGON station 5711, Colombia, 12° 13′ N, 72° 29′ W, 13 October 1965, 40-ft. fish trawl, 113 fathoms.

Paratypes: TABL 103026, (1 specimen) 194 mm SL, OREGON station 4453, Venezuela, 10° 54′ N, 67° 08′ W, 12 October 1963, 40-ft. flat trawl, 220 fathoms. TABL 103025, (1) 180 mm, OREGON station 4844, Colombia, 11° 06.7′ N, 74° 30′ W, 17 May 1964, 40-ft. flat shrimp trawl, 100 fathoms. TABL 101476, (13) 149–199 mm, (2, cleared and stained) 156–185 mm, (1, in Ionol) 183 mm; USNM 202746, (4) 158–184 mm; AMNH 26940, (1) 175 mm; ANSP 109542, (1) 177 mm; BMNH 1968.4.19.1, (1) 158 mm; CAS ...., (1) 180 mm; FMNH 74536, (1) 182 mm; MCZ 45996, (1) 181 mm; MNHN 1968–3, (1) 177 mm; RMHN 25916, (1) 180 mm; UMMZ 187315, (1) 177 mm, OREGON station 4843, Colombia, 11° 08.5′ N, 74° 29′ W, 17 May 1964, 40-ft .flat shrimp trawl, 100–120 fathoms. TABL 103027, (2) 188–190 mm, OREGON station 4913, Colombia, 12° 09′ N, 72° 47′ W, 1 June 1964, 40-ft. flat shrimp trawl, 100 fathoms. TABL 101723, (1) 197 mm, OREGON station 4914, Colombia, 12° 08′ N, 72° 41′ W, 1 June 1964, 40-ft. flat shrimp trawl, 75 fathoms. TABL 103024, (12) 195–219 mm; USNM 202745, (2) 202–204 mm, OREGON station 5711, collected with holotype. TABL 103004, (1) 73 mm, MISTY II, cruise 24, station 81, Florida, 25° 31′ N, 79° 52′ W, 24 March 1967, 100-ft. purse seine, surface to 17 ft. TABL 103003, (1) 65 mm, MISTY II, cruise 25, station 83, Florida, 25° 35.3′ N, 80° 02′ W, 8 April 1967, 100-ft. purse seine, surface to 17 ft. USNM 155271, (1) 117 mm, PELICAN station 204–4, Florida, 28° 56′ N, 80° 01.5′ W, 29 March 1940, 10-ft. try net, 100 fms.

Three specimens identified as *tabl* are not designated as paratypes, and the species description was not based on these three. One is partially digested, and was part of the stomach contents of a *Coryphaena hippurus*, caught trolling off North Carolina. The other two are very large specimens from St. Helena, and as yet there are no specimens of comparable size from the western Atlantic with which to compare them.

Etymology. An "arbitrary combination of letters" (International Code of Zoological Nomenclature, Appendix D. V.), *TABL*—The Tropical Atlantic Biological Laboratory of the Bureau of Commercial Fisheries established on Virginia Key, Miami, Florida, October 1965—to be treated as an indeclinable noun.

Relationships. The two specimens identified as *tabl* from St. Helena (BMNH 1868.6.15.14, 1910.9.9.18) are similar to four specimens (BMNH 1867.10.8.42–43, 1946.5.23.1–2) of "Stonebrass" (*fide* Cadenat and Marchal 1963: 1268) from St. Helena in numbers of lateral-line scales, but differ in having fewer gillrakers (11–12 + 31–32 *vs* 14–16 + 41–44).

D. tabl differs from *punctatus* in the western Atlantic and at Bermuda in lacking spots in the curved lateral line; in averaging more rays in the pectoral fin and fewer gillrakers (Table 3); in the shape of the lateral line (Fig. 5 *vs*. Fig. 4); in having more scales in the lateral line (Table 4); and in having a longer head and upper jaw, a shorter anal fin first spine, and a lower lateral-line ratio (Table 5).

D. tabl differs from *macarellus* in the western Atlantic and at Bermuda in averaging fewer anal fin softrays and lower limb gillrakers (Table 3); in the shape of the lateral line (Fig. 5 *vs*. Fig. 6); in having more lateral-line scutes, fewer anterior scales in the straight lateral line, and fewer total lateral-line scales Table 4); and in having a longer upper jaw, a longer dorsal fin first softray, and a longer anal fin first softray (Table 5).

DECAPTERUS PUNCTATUS (CUVIER)

ROUND SCAD

FIG. 2

Scomber Hippos (*non* Linnaeus): Mitchill 1818: 246 (misidentification; specimen from New York market, more than 8 in. long; specimen probably not now extant).

Caranx punctatus Cuvier, 1829: 208 (replacement name for Mitchill's 1818 *Scomber Hippos*; type specimen and type locality that of Mitchill's specimen).

Caranx punctatus Agassiz in Spix, 1831: 108, pl. LVI, fig. 2 (type locality Atlantic Ocean, probably along Brazil; two type specimens 5½–6 in. long, originally reported in Museo Monacensi, probably not now extant).

Caranx punctatus Cuvier in Cuvier and Valenciennes 1833: 38 (type locality Martinique; type specimens 6 pouces long, originally in MNHN).

Synonymy. In 1815, Mitchill illustrated (pl. V, fig. 5) *Decapterus punctatus*, but did not give a description or scientfic name, only captioning the figure as "Hippos Mackerel." Mitchill described the species in 1818 (p. 246–247), erroneously applying the name *Scomber Hippos* of previous authors, which applies to *Caranx hippos* (Linnaeus). Cuvier (1829: 208) wrote the following in a footnote: "*Car. punctatus*, N., nommé *Scomber hippos* par Mitch., Trans. de New-York, I, v, 5; mas qui n'est pas l'hippos de Linnaeus." Agassiz in Spix (1831: 108, pl. LVI, fig. 2) described and illustrated the species as *Caranx punctatus*, giving himself as author of that name and mentioning the pre-Linnean work on Brazilian fishes by Marcgrav, but not referring to the work of Mitchill or Cuvier (above). Cuvier in Cuvier and Valenciennes (1833: 38), described the species as "*Caranx punctatus*, nob.," based on specimens collected by M. Plée at Martinique, again citing Mitchill, but not mentioning his own earlier reference or that of Agassiz. Most authors have cited Agassiz as the author of the species, and in doing so, Bertin and Dollfus (1948: 10) listed Cuvier's 1829 use of *Caranx punctatus* as a *nomen nudum*. Cuvier (1829) is the author of the species, however, because his *Caranx punctatus* is the earliest available name. It satisfies the necessary articles of the International Code of Zoological Nomenclature: 10; 11 a, b, c, g; 12; 16 a, i and iii. Thus, the species was technically described as a new species three separate times, each with the identical binomial.

Diagnosis. A *Decapterus* with 10–14 spots on scales in a relatively short curved lateral line; scutes in posterior part of curved lateral line usually 1–5; scutes in straight lateral line 32–46; total lateral-line scales and scutes (excluding peduncle scales) 77–98; lateral-line ratio 0.92–1.16; gillrakers 11–16 + 32–44; pectoral softrays 18–20; vertebrae 10 + 15.

Description. Frequency distributions for significant meristic characters for western Atlantic specimens are shown in Tables 3 and 4. Ranges for significant morphometric characters of western Atlantic specimens are shown in Table 5. Total scales and scutes in the curved lateral line range 40–59, mean 49.5. Total scutes in the curved and straight lateral line range 34–49, mean 41.0. Straight lateral-line scales on the peduncle range 2–6, mean 3.5. Total scales and scutes in the lateral line (including peduncle scales) range 83–101, mean 92.0. Gillrakers over the hypobranchial range 11–16. Rudimentary gillrakers on the anterior ends of upper and lower limbs are usually absent, rarely one present on either limb. Vertebrae are 10 + 15 (212 specimens). The ultimate softray (finlet) of dorsal and anal fins is connected by a membrane to penultimate softray to about 45–50 mm SL. The curved lateral-line spots are concentrations of melanophores on the medial surface of pored scales in the lateral line; they are obviously forming on some specimens as small as 70 mm SL, and the usual complement of 12–14 spots is present on some specimens as small as 81 mm SL, but they are not apparent on other specimens as large as 119 mm SL (possibly due to inadequate preservation).

Size. The largest specimen examined from the western Atlantic (TABL 101748) is 183 mm SL, 8.4 in. TL, and weighs 109 gms. (0.24 lb.).

Distribution. Along the Atlantic seaboard from Nova Scotia to Rio de Janeiro, Brazil; throughout the West Indies; Bermuda. Available records indicate that this areal distribution is continuous. Smaller juveniles are pelagic and apparently prefer oceanic rather than neritic water over the continental shelf, but they may occur inshore around oceanic islands. Juveniles have been taken as far as 270 miles offshore. They remain pelagic to a size of *ca.* 80 mm SL, although they may be caught in bottom-fishing trawls as small as 45 mm. Larger juveniles and adults may be taken at the surface and close inshore, but most of the records of this study were taken in bottom-fishing trawls that were fishing in depths of 5 to 50 fathoms; and a 123 mm specimen was taken in a trawl that fished the bottom at 200 fathoms. Because these were not closing trawls and they could have caught the scad somewhere between the surface and the bottom, the depth records are uncertain. I presume for the records out to 50 fathoms that the fish were on or near the bottom, but, lacking additional records, I suspect that the 200-fathom record may represent a fish that was taken in midwater or above.

Relationships. D. punctatus has been distinguished from *tabl* under the account of that species. It differs from the other western Atlantic species, *macarellus,* in having spots along the curved lateral line and in the shape of the lateral line (Fig. 4 *vs.* Fig. 6); in having fewer pectoral fin softrays (Table 3); in having one more caudal vertebral centrum (15 *vs.* 14); and in being deeper-bodied between the second dorsal and first anal spine origins, and in having a longer pectoral fin, longer dorsal and anal fin lobes, and a longer anal fin first spine (Table 5).

D. punctatus in the western Atlantic is quite variable in certain characters, especially in numbers of lower limb gillrakers and scales in the curved lateral line; but these variations do not appear to be correlated with geographic location or sexual dimorphism. Specimens from Bermuda are considered to be conspecific with *punctatus* from the western Atlantic, although the small sample from Bermuda averaged slightly fewer softrays in the dorsal fin (31.1) and anal fin (27.1), and more gillrakers on the upper limb (14.4) and lower limb (38.9).

I consider the western Atlantic and Bermudan *punctatus* to be specifically distinct from its cognate along West Africa, at St. Helena, and other eastern Atlantic islands. The eastern Atlantic species averages more scales in the curved lateral line (46–63, mean 54.1, 59 specimens) and fewer scutes in the straight lateral line (30–38, mean 34.1, 62 specimens). This difference is reflected in the longer curved lateral line and correspondingly shorter straight lateral line of the eastern Atlantic species, which has a lesser lateral-line ratio (0.71–0.94) than *punctatus*.

I consider the valid name of the eastern Atlantic species that is cognate to the western Atlantic *punctatus* to be *Decapterus sanctaehelenae* (Cuvier), based on *Caranx sanctaehelenae* Cuvier in Cuvier and Valenciennes (1833: 37), type locality St. Helena. Cuvier stated (p. 38), "Nos individus sont longs de neuf pouces"—this equals *ca.* 243 mm TL. Bertin and Dollfus (1948: 10) reported 14 specimens from St. Helena in the Paris Museum to be syntypes of "*Caranx sanctaehelenae*" (which they considered to be a junior synonym of *Decapterus punctatus*). I examined these specimens in October 1965: MNHN 5852, 3 specimens, 151, 163 and 175 mm SL, collected by Quoy and Gaimard; MNHN 5948, 2 specimens, 163 and 172 mm SL, collected by Quoy and Gaimard; MNHN 5946, 8 specimens, 74–101 mm SL, collected by Dussumier; and MNHN 5947, 1 specimen, 192 mm SL and *ca.* 220 mm TL, collected by Lesson and Garnot. I herein designate as the lectotype of *Caranx sanctaehelenae* Cuvier the largest specimen from MNHN 5852, 175 mm SL, bearing a numbered tag tied to the lower jaw. In doing this, I have to disagree with Cadenat and Marchal (1963:1269), who considered that these specimens were not syntypes of Cuvier's *sanctaehelenae*, and applied that name to the "stonebrass" of St. Helena (a species that I diagnose as lacking spots in the curved lateral line, and having 14–16 + 41–44 gillrakers, 57–64 scales and no scutes in the curved lateral line, 34–38 scutes, and 95–103 total scales and scutes in the lateral line). By my interpretation, the St. Helena "stonebrass" lacks a valid scientific name.

DECAPTERUS MACARELLUS (CUVIER)

MACKEREL SCAD

FIG. 3

Caranx macarellus Cuvier in Cuvier and Valenciennes, 1833:40 (type locality Martinique; lectotype 256 mm SL, paralectotype 131 mm SL, both MNHN 5850).

Caranx Jacobaeus Cuvier in Cuvier and Valenciennes, 1833:42 (type locality Porto Praya, San Iago Id., Cape Verde Ids.; holotype MNHN 5849, 260 mm SL, *ca.* 295 mm TL).

Diagnosis. A *Decapterus* with a relatively long and low curved lateral line, lacking spots; 19–33 scales in anterior and 23–32 scutes in posterior part of straight lateral line; lateral-line scales and scutes (excluding peduncle scales) 119–133; gillrakers 9–13 + 32–39; pectoral softrays 21–23; vertebrae 10 + 14.

Description. Frequency distributions for significant meristic characters of western Atlantic specimens are shown in Tables 3 and 4. Ranges for significant morphometric characters of western Atlantic specimens are given in Table 5. Straight lateral-line scales on the peduncle range 6–13, mean 8.5. Total scales and scutes in the lateral line (including peduncle scales) range 126–140, mean 134.0. Gillrakers over the hypobranchial range 11–14. Rudimentary gillrakers on the anterior ends of the upper and lower limbs are usually absent, rarely one present on either limb. Vertebrae are 10 + 14 (21 specimens). No spots occur on scales of curved lateral line.

Size. The largest specimen examined was the lectotpye (MNHN 5850), 256 mm SL, *ca.* 295 mm or 11.6 in. TL. The next largest specimen examined from the western Atlantic (TABL 101731) is 247 mm SL, *ca.* 289 mm or 11.4 in. TL, and weighs 208 gms. (0.46 lb.).

Distribution. In the western Atlantic, known from (but not continuously) Nova Scotia to Fernando de Noronha off northeastern Brazil; at Bermuda; and in the eastern Atlantic at the islands of Cape Verde, St. Helena, Ascension, and in the Gulf of Guinea. Locations of specimens I have examined in the western Atlantic are quite dispersed: from the West Indies in the northern Bahamas, Porto Rico, Virgin Islands, Dominica, Martinique, and Grenadines; Curacao and Albuquerque Key in the Caribbean; and continental records from British Guiana, Colombia, Florida (off Miami), and Massachusetts. The available records suggest that this is primarily a pelagic and offshore species, and it is probably associated more with oceanic islands than continental areas. Three collections of the smallest juveniles were taken at the surface in the Gulf Stream off Miami. Larger specimens have been taken inshore with beach seines and pound nets (West Indies and Massachusetts); and the largest specimens examined were taken at the surface with a fish pump over 18 fathoms of water. One specimen was speared at a depth of *ca.* 12 fathoms over coral rubble. I have records of one specimen that was caught in a trawl on the bottom at 36–40 fathoms and another from 270 fathoms, but I assume that the latter, at least, was caught when the net was fishing well above the bottom.

Relationships. D. macarellus from the western Atlantic has been distinguished from *tabl* and *punctatus* under the accounts of those two species.

Based on available study specimens and literature accounts, I consider that only a single species of the *macarellus*-form exists in the Atlantic Ocean, and I tentatively record this as specifically distinct from a similar form or forms in the Indo-Pacific. Most recent authors have subscribed to the first consideration, but some have variously considered the Atlantic form to be the same species, or subspecies, or one or more distinct species from the Indo-Pacific named forms. Bertin and Dollfus (1948: 14–15) list the nominal Indo-Pacific species that have been included in synonymy of *macarellus*.

SPECIES AGGREGATIONS

In all of the individual collections of western Atlantic *Decapterus* I have examined, only a single species was present in each, with the exception of four collections. These exceptions were all from collections made off Miami, Florida, by James K. Dooley with a 100-ft. purse seine in the Gulf Stream *Sargassum* community. From April 1966 into May 1967, 102 such collections were made;

and 14 of those caught *punctatus* juveniles (34–80 mm SL). At two of these stations, both *punctatus* and *macarellus* were taken. At one station, both *punctatus* and *tabl* were taken. One station contained all three species: *punctatus* (89 specimens) 43–53 mm SL, *macarellus* (3) 50–62 mm, and *tabl* (1) 73 mm.

SPECIMENS EXAMINED

Decapterus tabl. North Carolina: (1) *ca.* 113 mm, TABL 103203, 34° 34′ N, 75° 19′ W, *ca.* 60 mi. E Cape Lookout, in stomach contents of female 675-mm FL *Coryphaena hippurus* (Linnaeus), caught surface trawling, 11 July 1954, GILL cr. 7, between reg. sta. 74 and 80. St. Helena: BMNH 1868.6.15.14, (1) 351, coll. J. C. Mellis; BMNH 1910.9.9.18, (1) 360, coll. J. T. Cunningham. Holotype and 51 paratypes (listed under the species account).

Decapterus macarellus. Massachusetts, USNM 13660, 20639, 38279, 38306, 82252, 84030. Florida Atlantic, TABL 103016, 103017, 103018. Colombia, TABL 103202. Guyana, BMNH 1961.9.1.21. Curacao, ANSP 52024. Alburqueque Key, ANSP 74159. Northern Bahamas, BMNH 1934.8.2.1–2; ANSP 108580. Porto Rico, UMML 2264, 8163; TABL 101730. Martinique, MNHN 5850 (lectotype 256 mm SL, paralectotype 131 mm SL). Dominica, TABL 101724. Cannouan, TABL 101731, 103319. West Indies, USNM 108388. Bermuda, FMNH 48341, 48411, 48412, 48535.

Decapterus punctatus. Massachusetts, USNM 16239, 58884, 58921, 77796, 120566, 128647. Delaware, USNM 187175. Western Atlantic from off North Carolina to off Georges Bank, USNM 189250, 189261, 189262, 189263, 189265, 189266, 189270–3, 189283, 189285, 189286, 189288, 189289, 189359. North Carolina, USNM 53117, 198996, 199019, 199026, 199034; TABL 101477, 101729, 101745, 101746, 101747, 101748, 101749, 101750, 101751, 101767, 101768, 101769, 101826, 101832, 102572, 102573, 102574, 102575, 102577, 102578, 102579, 102580, 102581, 102582, 102583, 102584, 102585, 102586, 102587, 102588, 102976, 102977, 102981, 102982, 103117. South Carolina, USNM 199013, 199016, 199024, 199032; TABL 101728, 101753, 101765, 101775, 101776, 101777, 101778, 101819, 101833, 102983, 102985, 102986, 102987, 102988, 103114, 103120. Georgia, USNM 199018; TABL 102570, 101727, 101773, 101779, 101784, 102978, 102980, 103119, 103127. Florida Atlantic, USNM 198995, 199012, 199042; TABL 101752, 101764, 101771, 101772, 101780, 101781, 101782, 101783, 101796, 101797, 101815, 102064, 102979, 103005, 103006, 103007, 103008, 103009, 103010, 103012, 103013, 103015, 103021, 103022, 103023, 103113, 103118, 103121, 103124, 103125, 103126. Florida Straits and Florida Keys, USNM 198973; TABL 101758, 101759, 101760, 101761, 103116. Florida Gulf, USNM 198976, 199020, 199021, 199022, 199029, 199037; FSBC 2689, 2728, 2927, 2968, 3069, 3434, 3597, 3700, 60–24, 62–56, 63–35; TABL 101785, 101999, 102062, 103122. Alabama, USNM 199015, 199017. Louisiana, TABL 101787. Texas, USNM 199014; TABL 101725, 102971. Mexico, Campeche, USNM 198993; TABL 101744, 102569. Mexico, Yucatan, TABL 102571. Honduras, TABL 102710. Costa Rica, TABL 101726. Panama, USNM 80037. Colombia, TABL 102568, 102972, 102973, 102974, 102975. Venezuela, TABL 102566, 102567, 102970. Guyana, BMNH 1961.9.1.11–20; TABL 101786, 102964, 102965, 102966, 102967. French Guiana, USNM 159822. Brazil, Maranhao, TABL 102969. Brazil, Bahia, USNM 43352: BMNH 1862.1.30. 41. Brazil, Rio de Janeiro, BMNH 1903.6.9.73, 1923.7.30.133–6. Blake Plateau, TABL 103115. Northern Bahamas, ANSP 102157; TABL 102984, 103123. Cuba, USNM 6028. Jamaica, LACM 5445. Porto Rico, USNM 126429, TABL 102565. Virgin Islands, TABL 102968. Anguilla Id., TABL 101789. St. Martin Id., TABL 101791. Dominica, TABL 101790. Martinique, TABL 103318. St. Lucia, TABL 101732, 103321. St. Vincent, BMNH 1931.12.5.306–7. Bequia, TABL 101733, 103313, 103317, 103320. Canouan, TABL 103312. Carriacou, TABL 103309. Grenada, TABL 101792, 103310, 103311. Barbados, TABL 103315. Tobago, USMN 190507, BMNH 1920.12.22.41–44, 1922.6.22.56; TABL 103314. Trinidad, TABL 103316. Eastern Caribbean, TABL 102564. Bermuda, USNM 10334, 21365, 160980, 178417, 251937; BMNH 1872.8.28.37, 1879.10.9.47; ANSP 52337–8.

GENERIC RELATIONSHIPS

The morphological characteristics and limits of the genus *Decapterus* are not as yet adequately defined. The same is true for the genus *Caranx* Lacépède 1802, and other associated genera. Precise definition and restriction and species allocation must await thorough analysis of all species concerned.

In their review of the genus, Bertin and Dollfus (1948) included 7 species in the genus *Decapterus*, but 2 of these relate to other genera: 1) *Caranx suareus* Risso in Cuvier and Valenciennes, 1833:33 (type locality Nice, France; holotype 435 mm SL, MNHN B. 869) with the following included as a junior synonym, *Decapterus longimanus* Norman 1935:255 (type locality Tristan de Cunha; holotype 412 mm SL, BMNH 1935.5.2.3). Both of these nominal species relate to the genus *Trachurus* Rafinesque, 1810, and *suareus* was correctly related to *Trachurus* by Blanc and Bauchot (1961:491). 2) *Decapterus normani* Bertin and Dollfus 1948:21 (type locality Madagascar; holotype 254 mm SL, MNHN 47–7). This is a junior synonym of *Atule mate* (Cuvier in Cuvier and Valenciennes 1833:54), as defined by Williams (1958:378).

Bertin and Dollfus (1948:9) included as one of their 7 species of *Decapterus*, *Caranx rhonchus* Geoffrey St. Hilaire 1809. I concur with this generic placement, although Blanc and Bauchot (1961:491) considered *rhonchus* to be a species of *Caranx*.

Suareus furnestini Dardignac and Vincent in Furnestin *et al* (1958:445), described as a new genus and species related to *Trachurus*, was correctly included in *Trachurus* by Blanc and Bauchot (1961:491).

Two other genera form a closely-related complex with *Decapterus*—*Trachurus* and *Selar* Bleeker 1850. [I follow Ginsburg (1952:83) in recognizing *Trachurops* Gill 1862, as a junior synonym of *Selar*.] These 3 genera can be distinguished from other Caranginae by the following combination of characters: 1) Scales present on all 4 pairs of opercular bones, on interorbital region, and usually on maxillae; chest completely scaled. 2) First 2 anal spines of similar length, the first usually longer, or sometimes slightly shorter, than the second; the second definitely not much longer than the first. 3) Teeth usually present in a band on tongue, on both head and shaft of vomer, and frequently on head of palatines; small teeth present on both jaws, either in a single row or a narrow band. 4) No bilateral, paired keels on caudal peduncle.

The three genera can be distinguished by the following combination of characters.

1a) Pored scales in curved lateral line expanded dorsoventrally, scute-like, *Trachurus*.
1b) Pored scales in curved lateral not so expanded, about as long as high, *Selar* and *Decapterus*.
2a) A single-rayed finlet present at end of dorsal and anal fins, or the terminal finray having a greater distance between it and penultimate ray than between more anterior rays, *Decapterus* and *Trachurus*.
2b) Terminal fin ray of dorsal and anal fins close to penultimate ray, not greatly displaced or forming a finlet, *Selar*.
3a) Bilateral dorsoposterior accessory lateral lines converging and ending at end of supraoccipital crest, *Decapterus*.
3b) Accessory lateral lines extending to origin of first dorsal fin or beyond, *Trachurus* and *Selar*.
4a) Two fleshy papillae on shoulder present or lacking, if present neither especially enlarged, *Decapterus* and *Trachurus*.
4b) Two fleshy papillae present on shoulder girdle, the lower enlarged with a furrow formed at its ventral surface, *Selar*.

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A NEW SPECIES OF SARDINE (*SARDINELLA*, CLUPEIDAE) FROM THE MARQUESAS ISLANDS[1]

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A sardine from the Marquesas Islands in recent years has been introduced to the Hawaiian Island area as a bait fish and has successfully reproduced there. A study has been completed on many aspects of its biology (Nakamura and Wilson, MS). In several publications this species has been referred to or discussed under the name *Harengula vittata* (Valenciennes) and other binomials (see synonymy).

Of the three closely related genera *Sardinella, Herklotsichthys,* and *Harengula,* the Marquesan sardine is best included in *Sardinella,* as defined by Chan, 1965a, Berry, 1964, and Whitehead, 1963 and 1964.

Recent studies of the Indo-Pacific species of *Sardinella* have better defined many of the valid species and have clarified the status of many nominal species (Dutt, 1959 and 1961; Chan, 1965a and 1965b; Whitehead, 1965 and 1966; Whitehead, Boeseman, and Wheeler, 1966; Whitehead, 1967). We find that the Marquesan sardine lacks a valid scientific name, and we describe it here as a new species.

Sardinella marquesensis new species

Figs. 1–6

Harengula sundaica (*non* Bleeker), Kendall and Goldsborough, 1911:243 (specimens from Nukahiva, MCZ 29507 and USNM 50794).

Sardinella jussieu (*non* Lacépède), Fowler, 1928:30 (in part; based on Nukahiva specimens, USNM 65861; excluding other references and distributions).

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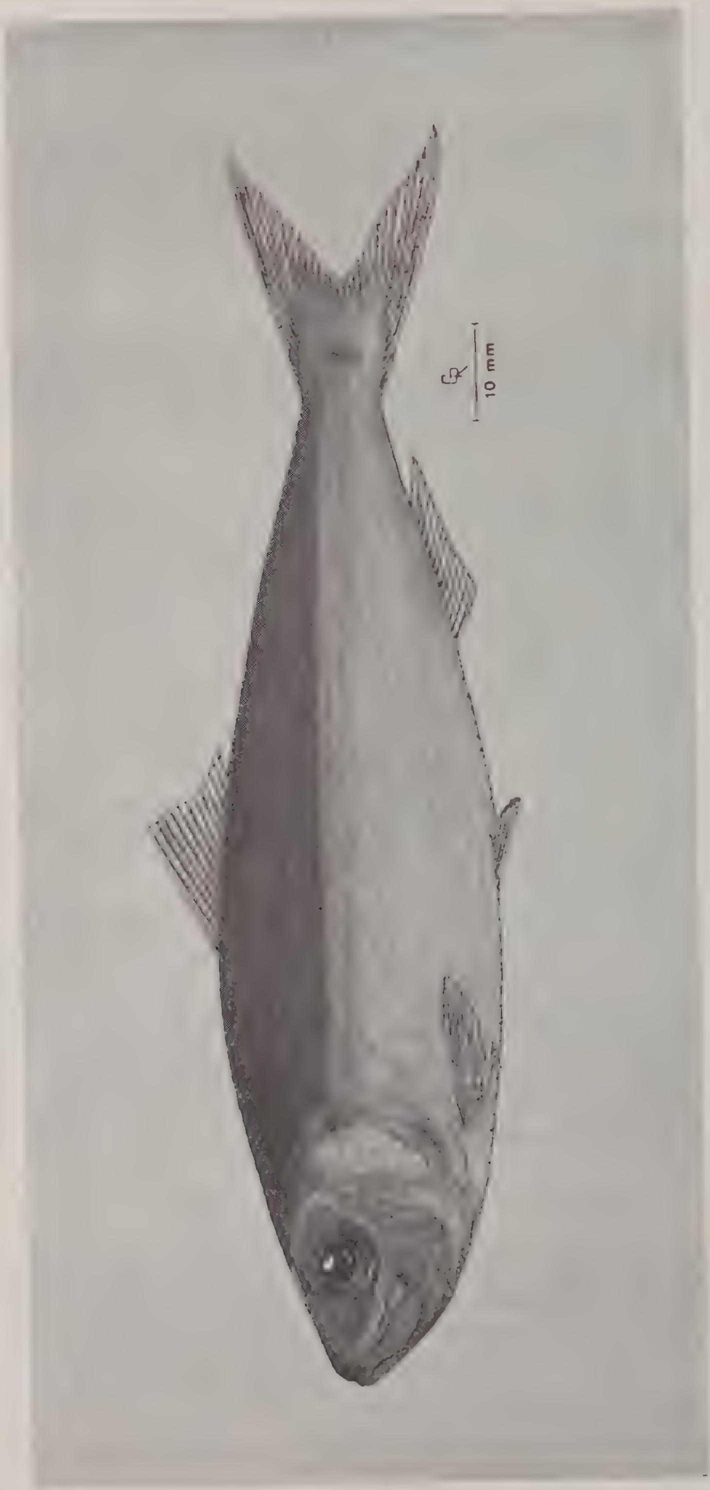

FIGURE 1. *Sardinella marquesensis*, holotype, 107 mm SL, Taiohae, Nuku Hiva, Marquesas Islands, USNM 201946.

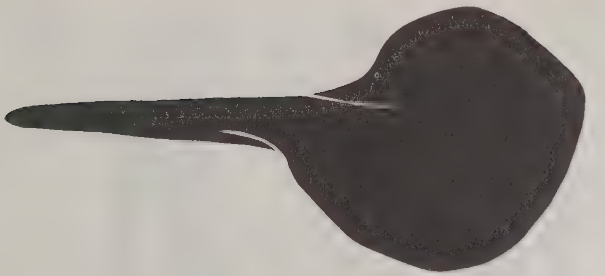

FIGURE 2. Outline of second (posterior) supramaxilla of S. *marquesensis*. The anterior (shaft) end is to the left.

Sardinella melanura (*non* Cuvier), Fowler, 1928:30 (in part; based on Nukahiva specimens, MCZ 29507; excluding other specimens and references).

Harengula vittata (*non* Valenciennes), Fowler, 1941:596 (in part; based on Nukahiva specimens, USNM 65861; excluding other references). Wilson and Rinkel, 1957:110 (the Marquesan sardine, caught as a bait species). Wilson, Nakamura, and Yoshida, 1958:71 (Marquesan bait species). Murphy, 1960:185 (introduction into Hawaiian waters). Yoshida, 1960:37 (Marquesan bait species). Hida and Morris, 1963: 431 (Marquesan sardine in Hawaii).

Diagnosis: A *Sardinella* with overlapping scales on median predorsal ridge (not a single median row); 8 pelvic finrays; body scales with 3 to 6 anterior interrupted transverse grooves, and with exposed portion not perforated, greatly produced, or fimbriated; 58 to 85 gillrakers on lower limb of first arch (at 80 to 107 mm SL); no dark tips on caudal fin lobes. Supplemental diagnostic characters: Head length 25.5 to 28.3% SL (3.5 to 3.9 times into SL); body depth 22.9 to 28.5% SL (3.5 to 4.4 times into SL); 16 or 17 prepelvic and 12 or 13 postpelvic ventral scutes; ca. 30 to 60 epibranchial and ca. 23 to 35 ceratobranchial gillrakers on first arch (at 80 to 107 mm SL).

Holotype: USNM 201946, 107 mm SL, caught at Taiohae Bay, Nuku Hiva, Marquesas Islands, 08°55′ S, 140°06′ W, 14 September 1956, on *Charles H. Gilbert* cruise 30, station 45, by bait seine, preserved by Donald W. Strasburg.

Description of the Holotype: Dorsal rays 17. Anal rays 21. Pectoral rays 14 on each side. Pelvic rays 8 on each side. Lateral scale rows ca. 42. Transverse scale rows ca. 12. Ventral scutes: prepelvic 16, postpelvic 12. Frontoparietal striae ca. 7 on each side. Gillrakers on lateral side of first arch, epibranchial 39, ceratobranchial 30, hypobranchial ca. 41. Branchiostegals 7 on each side. Pseudobranchial filaments 15. Gill filaments on lateral side of first arch, upper limb ca. 25, lower limb ca. 45. [Measurements in millimeters, followed by percent of standard length in parentheses:] Standard length 107. Fork length 115 (107.5). Total

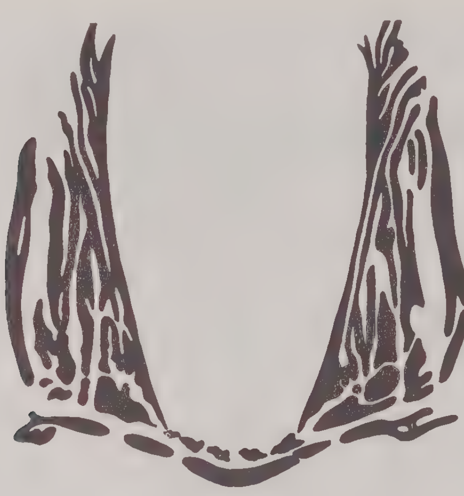

FIGURE 3. Outline of the striae on the frontoparietal and occiput region of S. *marquesensis.*

length 130 (121.5). Head length 28.0 (26.2). Eye diameter 7.9 (7.4). Pupil diameter 3.6 (3.4). Snout length 8.0 (7.5). Upper jaw length 11.7 (10.9). Lower jaw length 13.7 (12.8). Opercle depth 14.5 (13.6). Pseudobranch length 6.6 (6.2). Gillraker length, at angle on lower limb 4.9 (4.6). Longest dorsal ray length (5th) 15.3 (14.3). Dorsal-fin base length 15.2 (14.2). Longest anal ray length (4th) 4.7 (4.4). Anal-fin base length 16.6 (15.5). Pectoral fin length 16.9 (15.8). Pelvic fin length 11.6 (10.8). Pelvic axillary scale length 8.5 (7.9). Snout to dorsal-fin origin 47.5 (44.4). Snout to pelvic-fin origin 53.5 (50.0). Snout to anal-fin origin 77 (72.0). Dorsal-fin origin to caudal base 62 (57.9). Body depth, at occiput 22.0 (20.6), at dorsal-fin origin 28.2 (26.4), at anal-fin origin 20.3 (19.0), least depth of peduncle 9.8 (9.2). Body width at dorsal-fin origin 12.4 (11.6).

Paratypes: MARQUESAS ISLANDS. Nuku Hiva, Taiohae Bay, 08°55′ S, 140°06′ W, *Gilbert* cruise 35, station 11, 13 October 1957, ANSP 109213 (1 specimen, 95 mm SL), BMNH 1967.11.4.1–2 (2, 95–103), BPBM 5592 (1, 98), CAS 24046 (1, 101), FMNH 74076 (1, 85.5), RMNH 25824 (1, 95), MCZ 45899 (1, 98), MNHN 1967-591 (1, 105), SU 66228 (1, 97), TABL 101827 (2, 93–101), UMMZ 186866 (1, 95), USNM 201947 (2, 88–106). Hiva Oa, Atuona, 09°49′ S, 139°03′ W, *Gilbert* cruise 32, station 26, 27 January 1957, ANSP 109212 (1, 62), BMNH 1967.11.4.3 (4, 53–59.5–62–67), BPBM 5593 (2, 60.5–63), CAS 24045 (2, 62–63.5), FMNH 74075 (1, 62), RMNH 25825 (2, 58.5–64.5), MCZ 45898 (1, 62), MNHN 1967-590 (2, 60–63.5), SU 66229 (1, 59.5), TABL 101828 (3, 48.5–55.5–67), UMMZ 186867 (1, 62), USNM 201948 (3, 53.5–56.5–64). Nuku Hiva, Taiohae Bay, collected with the holotype, USNM 179874 (19, 56.5–96.5). Nuku Hiva, Taiohae

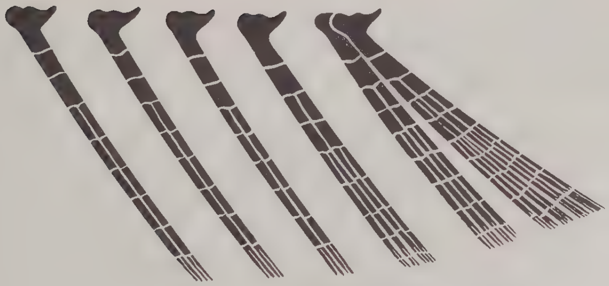

FIGURE 4. Outline of posterior 5 anal-fin rays of *S. marquesensis.*

Bay, 08°55′ S, 140°06′ W, *Gilbert* cruise 43, station 90, 14 March 1959, TABL 101829 (7, 77.5–91). Tahu Ata, Vai Tahu, 09°07′ S, 139°06′ W, *Gilbert* cruise 50, station 33, 24 November 1960, TABL 101830, (39, 45.5–97.5). Nuku Hiva, Taiohae Bay, 08°55′ S, 140°06′ W, *Gilbert* cruise 50, station 32, 22 November 1960, TABL 101831 (26, 74–88). Nuku Hiva, Taiohae, 26 September 1929, ANSP 52615 (1, 59). Nuka Hiva, 17 September 1899, USNM 65861 (25, 33.5–61.5), MCZ 29507 (7, 43–52).

Description of the Species: Dorsal-fin rays 16 (7 specimens) or 17 (22); the first 3 or usually 4 rays unbranched; the last ray divided to its base. Anal-fin rays 18 (1), 19 (16), 20 (11), or 21 (1); the first 3 or rarely 2 rays unbranched; the last ray divided to its base. Pectoral-fin rays 13 (4), 14 (20), or 15 (17) on the left side; of 41 specimens, 6 with one more ray on right side than on left, 3 with one more ray on left; the first ray unbranched. Pelvic-fin rays 7 on both sides (39), 8 on left side and 7 on right (1), and 7 left and 8 right (1); the first ray unbranched. Caudal-fin rays 10 + 9 principal, 9 or 10 + 7 or 8 secondary. Branchiostegal rays 6 on both sides (41), 6 left and 7 right (3). Scales in lateral series ca. 35–42 (no specimens with all scales remaining). Ventral scutes, 16 prepelvic + 12 postpelvic (1), 17 + 12 (22), 17 + 13 (15). Gill filaments on lateral side of first arch ca. 21 to 25 upper and 40 to 45 lower at 88 to 107 mm SL. Pseudobranchial filaments ca. 14 to 19, tending to increase with increase in body length.

Body proportions in percent of standard length from 11 selected specimens 67–107 mm SL, except as noted. Head length 25.5 to 28.3 (as in diagnosis). Eye diameter 7.3 to 8.2. Snout length 7.2 to 8.1. Upper jaw length 10.9 to 11.6. Lower jaw length 12.1 to 13.6. Pectoral-fin length 15.8 to 17.6. Pelvic-fin length 10.7 to 12.2. Pelvic axillary scale length 6.9 to 8.2. Dorsal-fin base length 11.5 to 15.1. Anal-fin base length 14.3 to 16.5. Snout to dorsal-fin origin 43.4 to 47.3. Snout to pelvic-fin origin 50.0 to 54.2. Snout to anal-fin origin 72.0 to 76.8. Caudal base to dorsal-fin origin 55.7 to 59.0. Caudal base to pelvic-fin origin 52.4 to 55.2. Caudal base to anal-fin origin 27.0 to 30.4. Depth at occiput 20.4 to 23.1. Depth at dorsal-fin origin 24.8 to 27.1, tending to increase slightly with increase in body length. Depth at anal-fin origin 17.5 to 20.0. Least depth of peduncle 9.1 to 10.2. Body width at dorsal-fin origin 10.1 to 11.6. Length of gillraker at angle on lower limb 4.0 to 5.1.

Body compressed, the belly strongly keeled. Snout usually slightly shorter than eye diameter. Maxilla smooth along lower edge; the second (posterior) supramaxilla somewhat rounded posteriorly, but with the point of junction at the shaft of the ventral part of the expanded portion anterior to that of the dorsal part (Fig. 2); no hypomaxilla. No teeth in upper jaw or on palate or tongue; a few recurved canines near symphysis of lower jaw. Upper jaw ending at about a vertical through the anterior part of the pupil.

Pseudobranch with crescentic base and a slightly elevated basal ridge; its length about equal to eye diameter. Gillrakers relatively slender, tapering markedly at anterior ends of upper and lower limbs. Fronto-parietal region (Fig. 3) as described under generic relationships. Branchiostegal membrane on left side overlapping externally at isthmus with that on right side.

Dorsal and anal fins with low scaled basal sheaths; dorsal-fin origin nearer to tip of snout than to caudal base; anal-fin origin about midway between pelvic-fin origin and caudal base, or slightly nearer to pelvic; last 2 rays of anal fin not markedly enlarged but more branched than preceding rays (Fig. 4). Pectoral–fin tips failing to reach pelvic-fin origin by a distance greater than snout length and less than post-orbital head length; a recess present beneath dorsal part of pectoral fin. Pelvic-fin origin beneath about anterior third or fourth of dorsal-fin base; pelvic fin inserted about midway between pectoral-fin origin and anal-fin origin or slightly closer to anal fin; pelvic axillary scale present, its length about three-fourths that of pelvic fin. Scales covering bases of pectoral, pelvic, and caudal fins, extending onto dorsal and anal lobes of caudal fin to near fork of fin.

Body scales. Exposed portion only slightly eroded or not eroded posteriorly and not fimbriated, and lacking perforations (Fig. 5). Anterior (imbedded) portion of scale with a continuous basal transverse groove and with the more anterior transverse grooves all interrupted and increasing in number both from anterior to posterior part of the body and with increase in length of fish. Scales from the midlateral side of the body, on a 103-mm specimen with 2 to 4 anterior interrupted transverse grooves anterior to the dorsal-fin origin, 4 or 5 between the origins of the dorsal and anal fins, and 5 or 6 on the peduncle. Scales taken from peduncle with 2 anterior interrupted grooves on a 31-mm specimen, 4 at 70 mm, and 5 or 6 at 103 mm.

Predorsal scales. Scales between the occiput and the dorsal-fin origin along the middorsal ridge are not arranged in a single median row typical of the subgenus *Amblygaster* (Chan, 1965a:106; 1965b, Fig. 1). Neither are they exactly as described as "a double row" for the subgenus *Clupeonia* (Whitehead *et al.,* 1966:47; Chan, 1965a, 1965b). They are

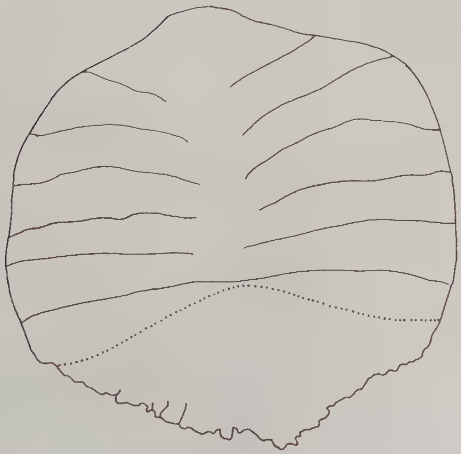

FIGURE 5. Scale from the midlateral part of the body above the anal-fin base of S. *marquesensis*. The imbedded portion is at the top; the dotted line marks the termination of the circuli.

basically irregular and not strictly median. In one 95-mm paratype, 19 scale-pockets (scales missing) lie in part over the median predorsal ridge; 8 of them are mainly on the left side of the fish, 6 are on the right, and 5 are essentially median; the 5 median scales are in consecutive series starting about one-half way back in the area. Other type specimens have similar but varying arrangements of predorsal scales.

Pigmentation. Dorsal third of body darkly pigmented, usually marked in its ventral portion by a slightly wide and a narrow longitudinal stripe, and grading into small, less dense melanophores on the midlateral part of the body, with the ventral third to half of the body unpigmented. Top of head and snout dark, with melanophores grouped along anterior part of preorbital, premaxilla, and maxilla, and along mandible; melanophores scattered below eye and on opercular bones; tip of lower jaw and frenum dark. Dorsal and caudal fin with scattered melanophores; pectoral, pelvic, and anal fins unpigmented. Peritoneum very dark. Scattered melanophores on tongue, inside mandibles, on palate, on inside of gill covers (especially grouped along pseudobranch base), and in humeral area beneath gill cover. No marked spots on body; the two stripes mentioned above not very pronounced, and not obvious or formed on smaller specimens; the caudal fin without dark tips on the lobes.

Gillrakers. The number of gillrakers on the lateral side of the first gill arch increases with increase in body length. This increase is depicted for a series of specimens between 31 and 107 mm SL in Fig. 6. The gillrakers on the upper limb (over the epibranchial bone) are shown on the top portion of the graph; the stippled area indicates our estimation, from this relatively small sample, of the number of gillrakers that might be expected at any standard length within this size range. The lower

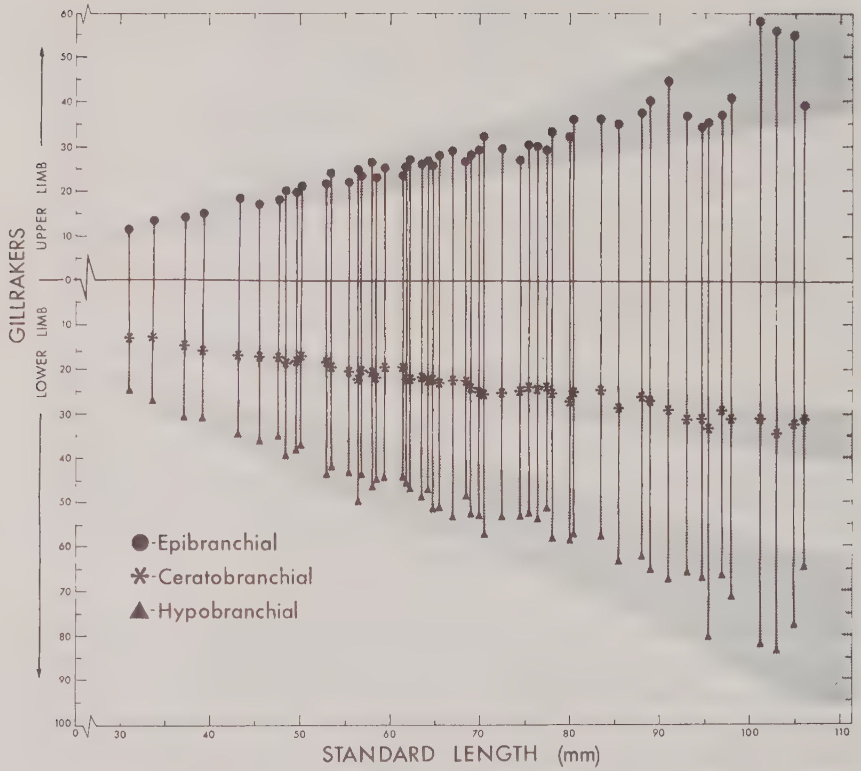

FIGURE 6. Depiction of gillraker ontogeny in S. *marquesensis,* showing the number of gillrakers located over each element of the first gill arch (epibranchial above; ceratobranchial and hypobranchial cumulatively below) for 52 specimens of various standard lengths.

portion of the graph shows the number of gillrakers (increasing downward on the graph) on the lower limb (i.e., over the ceratobranchial and hypobranchial bones); the number of gillrakers over the hypobranchial has been added to that over the ceratobranchial for each specimen (this number is associated above with the epibranchial count for each specimen); the number of gillrakers plotted for hypobranchial thus represents the total number of gillrakers on the lower limb. The stippled areas again represent the estimated range in number of rakers that might be expected at any standard length. The increase in number of gillrakers over the epibranchial and hypobranchial bones is expected, because the small, graduated rakers over the anterior ends of each of these bones indicates that these are the areas of continued formation of additional gillrakers. The stippled area representing the complement of gillrakers over the ceratobranchial bone also indicates an increase in gillraker number with increase in standard length; but because of the relatively similar lengths of gillrakers over the ceratobranchial, it is apparent that no new gillrakers can be formed there. We theorize that the increase over the ceratobranchial is produced by the growth anteriorly of the bone so that its anterior end comes to lie under gillrakers that previously were over the posterior end of the hypobranchial. A similar condition was observed in the thread herring genus *Opisthonema* (Berry and Barrett, 1963).

On the basis of our estimates of gillraker complements, the following number of gillrakers could be expected at the body sizes indicated:

Standard length	*30*	*40*	*50*	*60*	*70*	*80*	*90*	*100*
Epibranchial	9–13	13–20	17–25	21–29	24–34	26–40	29–48	33–58
Ceratobranchial	11–15	13–18	16–21	18–25	20–28	22–31	24–35	27–38
Lower limb	21–26	27–35	34–45	40–53	44–61	49–70	54–81	59–89

Occurrence or absence of gillrakers on the five gill arches in S. *marquesensis* is typical of that in other species of *Sardinella.* An 88-mm SL specimen of S. *marquesensis* had the following numbers of upper + lower limb gillrakers on the lateral and medial sides of the 5 arches:

arch	*lateral*	*medial*
1st	37 + 62	0 + 0
2nd	39 + 80	0 + 0
3rd	37 + 65	24 + 0
4th	26 + 48	56 + 30
5th	54 + 30	———

Vertebrae. Forty-two vertebrae (including the terminal ural) in 79 specimens. Two other specimens had 43 vertebrae, but both had abnormal structures associated with the centra. Six other specimens had 44 vertebrae; 5 of these were abnormal, but the sixth specimen apparently had normal structure. X-rays show usually 9, rarely 8, supraneurals (predorsals) anterior to the interneurals.

Distribution: S. *marquesensis* was apparently endemic in the Marquesas, from where it was first recorded in 1899. In 1957 it was introduced into Hawaiian waters. It is the only known species of Clupeidae occurring in the Marquesas Islands, where it apparently replaces the closely related S. *melanura,* widely distributed from the Society Islands westward into the Indian Ocean.

Relationships with Other Species: Sardinella marquesensis is most closely related to *Sardinella melanura* (Cuvier, 1829), a species with prominent black tips on the lobes of the caudal fin. Chan (1963b:7) described S. *nigricaudata* as a new species from New Hebrides, making three Indo-Pacific species of the *Sardinella-Herklotsichthys* group with black-tipped caudal-fin lobes; the other two, long acknowledged species were S. *melanura* (Cuvier) and *Herklotsichthys vittata* (Valenciennes, 1847). Whitehead (1967) concluded that *vittata* of Valenciennes was a junior synonym of *melanura* of Cuvier, questioned the validity of *nigricaudata* of Chan, and suggested that there was only a single, wide-ranging species with black caudal tips (i.e., *melanura*) from the Indian Ocean and the Philippines to Tahiti. Currently we subscribe to Whitehead's suggestion. We further add that all specimens we have seen of S. *melanura,* from throughout its range, have no appreciable variation in the black-tipped lobes.

S. *marquesensis,* with one exception, is similar in morphological characters to S. *melanura.* Compared to specimens of S. *melanura* (ANSP 86245) from Tahiti (about 750 miles from the Marquesas Islands), S. *marquesensis* has slightly greater gillraker complements and tends to have a less deep body, especially under the termination of the dorsal fin. The black-tipped caudal-fin lobes that characterize S. *melanura* are absent in S. *marquesensis.* The scarcely and uniformly pigmented lobes of S. *marquesensis* (and the lack of black tips) are constant not only in the type specimens we have examined, but also in all live specimens observed by Bureau of Commercial Fisheries personnel in the Marquesas and in progeny of that stock that has reproduced in Hawaiian waters (E. L. Nakamura, personal communication). We conclude that this striking difference in caudal pigmentation between the two species represents a trenchant genetic difference, and requires specific distinction of the two forms.

Generic Allocation: Most of the morphological characters proposed to separate the genera *Sardinella, Herklotsichthys,* and *Harengula* are subjective, and most of these characters are not precise (as they have been defined) in certain species within these genera. This statement holds particularly in *Sardinella marquesensis,* which is more intermediate in characters between *Sardinella* and *Herklotsichthys* than other species previously studied as critically. [These two genera lack the hypomaxillae, present in the American *Harengula;* hence the latter need not be further considered here.] The four characters used in recent publications to distinguish between *Sardinella* and *Herklotsichthys* are discussed below in relation to S. *marquesensis.*

1. Relative size of terminal two anal-fin rays: in *Sardinella* more extensively branched and elongated than preceding rays; in *Harengula* relatively similar in size and branching to preceding rays. This character was used by Regan (1917) and was qualified by Chan (1966a:107–109). In some species of *Sardinella* the excessive branching, thickness, and length of the last two anal-fin rays are extremely pronounced, whereas in *Herklotsichthys* the last several rays are almost identical to those preceding, and the antepenultimate ray may be longer than the penultimate ray (except that the terminal ray is branched to its base). In other species of *Sardinella* the last two rays are almost intermediate between these two extremes. In S. *marquesensis,* the antepenultimate ray is the same length as or slightly longer than the penultimate ray (but not as long as the ultimate ray), but the two terminal rays are slightly thicker and more branched than those immediately preceding (Fig. 4). In this character, S. *marquesensis* is almost intermediate between the two genera.
2. Transverse grooves on body scales: the basal transverse groove is

continuous in both genera; in *Herklotsichthys* the other (anterior) transverse grooves in the anterior field are reported to be continuous from dorsal to ventral margin of the scale on *all* scales from the midlateral side of the body; in *Sardinella* the other transverse grooves are interrupted on body scales of all species in the area anterior to a vertical of the dorsal-fin origin (in some species transverse grooves are interrupted on all body scales, but in other species the grooves may be partially or incompletely interrupted in the area posterior to a vertical of the dorsal-fin origin, Chan, 1965a: 107–109); *S. marquesensis* has all grooves (other than the basal transverse groove) interrupted on all midlateral body scales (Fig. 5). This character would imply, on the basis of previous accounts, a relation only to *Sardinella,* and would exclude *Herklotsichthys.* We know, however, that previous accounts are partly erroneous, because certain midlateral body scales posterior to the cleithrum and anterior to a vertical of the dorsal-fin origin in *Herklotsichthys* (two species examined, as well as four species of *Harengula*) have interrupted transverse grooves. This observation tends to discount further the morphological and taxonomic separation of *Herklotsichthys* from *Sardinella.*

3. Shape of the second supramaxilla: in *Sardinella* the junction of the shaft of the second supramaxilla with its expanded posterior portion is aligned almost dorsally and ventrally and the dorsal and ventral parts of the expanded portion are almost equal in area (described variously as rectangular, almond-shaped, paddle-shaped, nearly circular); in *Herklotsichthys* the point of junction of the ventral part of the expanded portion is well anterior to that of the dorsal part, and the ventral part is larger than the dorsal (described as somewhat crescentic) (Chan, 1966a:108–109). This character is also subjective to a degree, as the shape of the expanded portion of some species of *Sardinella* departs from the "nearly circular" shape toward that of *Herklotsichthys.* Here again, *S. marquesensis* tends to be intermediate (Fig. 2); most of the expanded portion has a nearly circular outline as in *Sardinella,* but the ventral part of the expanded portion joins the shaft distinctly anterior to the junction of the dorsal part—characteristic of *Herklotsichthys.*
4. Number of fronto-parietal striae: cited as 3–7 in *Herklotsichthys;* 7–14 in *Sardinella* (Whitehead, 1964:41). The individual striae are easier to distinguish and to count in some species of the two genera than in others. In *S. marquesensis* they are especially confused; there is much branching and anastomosing, and more irregularity in thickness in the striae (Fig. 3) than in most other species examined; and they are even less well-defined in larger than in smaller specimens. Our approximate counts of the striae in *S. marquesensis* range from six to eight on one side, which is intermediate between the ranges given for the two genera, but the high count of eight favors *Sardinella.*

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Migration and Survival of Redfish Lake, Idaho, Sockeye Salmon, *Oncorhynchus nerka*

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Migration and Survival of Redfish Lake, Idaho, Sockeye Salmon, *Oncorhynchus nerka*

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ABSTRACT

Most adult sockeye salmon returning to Redfish Lake had spent two years in the ocean. Survival from smolt to returning adult at the lake ranged from 0.14 to 1.83%. The sex-ratio was nearly even.

Survival of sockeye in the lake from potential egg deposition to smolt migration was usually less than 6%. In at least one year, smolts originating from kokanee and/or residual sockeye may have comprised a large proportion of the migration. There was little relationship between egg deposition and smolts produced.

Sockeye salmon smolts migrated from Redfish Lake primarily from 1800 to 2400 hr. There was no consistent relationship between seasonal timing of the migration, lake ice cover, temperatures or flow of the outlet stream. The role of photoperiod in timing of the migration and the parr-smolt transformation is unclear.

Growth of juvenile sockeye in the lake was inversely related to population density and age at migration was dependent upon first year growth in the lake. More than half the fish of a year class migrated as yearlings when their mean length was more than 85 mm. When the mean length of yearlings was less than 85 mm less than half the fish of a year class migrated as yearlings.

INTRODUCTION

Redfish Lake, at the headwaters of the Salmon River, is the only lake in Idaho still used annually by sea-run sockeye salmon (*Oncorhynchus nerka*) for spawning and freshwater rearing. Information on the survival, age, and size of migrants, and the timing of the migrations of Redfish Lake sockeye salmon is presented. These studies of the Redfish Lake sockeye salmon were initiated after increased numbers of sea-run fish were observed at the lake after a period of absence and information was needed to manage the stocks.

Redfish Lake is the largest of a group including Stanley, Yellowbelly, Pettit, and Alturas lakes that formerly contained sockeye salmon. The lake is at an elevation of 6,500 feet and is 897 miles from the Pacific Ocean *via* the Columbia, Snake, Salmon Rivers, and Redfish Lake Creek (Figure 1). The lake is about 4 miles long, ¾ mile wide, and as much as 300 feet deep. It is a relatively infertile, oligotrophic lake with total dissolved solids of less than 60 ppm (Casey and Webb, 1960).

The number of adult sockeye returning to Redfish Lake in recent years (less than 5,000 fish annually) is probably only a small fraction of the number which returned during the 1800's. Evermann (1895 and 1896) visited the lakes at the headwaters of the Salmon River in 1894 and 1895. His observations and discussions with local residents led him to believe that these lakes were very important as spawning and rearing areas for Columbia River sockeye salmon. He reported that there were even plans, at one time, to build a cannery at Redfish Lake to process the sockeye catch. There is no reliable information on the numbers of sockeye salmon spawning in the Redfish Lakes at those early times.

ORIGIN OF PRESENT ANADROMOUS STOCK

The present stock of sockeye salmon spawning in Redfish Lake is probably not genetically identical to the indigenous stock because of an interrupted passage to the lake during the

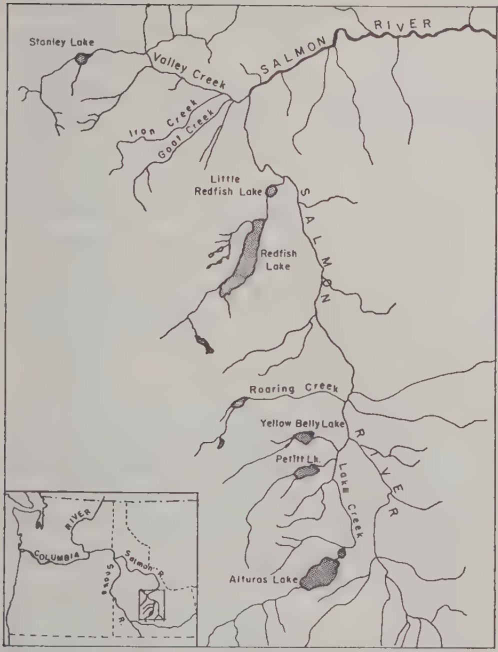

FIGURE 1.—The location of Redfish Lake at the headwaters of the Salmon River, Idaho.

early 1900's. Sunbeam Dam, built in 1913 on the main Salmon River approximately 20 miles downstream from the mouth of Redfish Lake Creek (Parkhurst, 1950), constituted a serious if not complete barrier to salmon migrations for many years. Attempts to construct fishways around the dam were never successful and sockeye salmon were reportedly unable to pass upstream (Locke, 1929). The dam was partially removed in 1934 to permit the passage of salmon.

Sea-run sockeye salmon were reported in Redfish Lake in 1942 (Parkhurst, 1950). Hauck (1955) listed the following possible explanations for the reestablishment of sockeye salmon in Redfish Lake: (1) a few fish were able to ascend Sunbeam Dam either through the inadequate ladder or through the tunnel; (2) sockeye salmon continued to spawn in the river below Sunbeam Dam during the years they were blocked and returned to the lake after removal of the dam; (3) the sockeye salmon originated from a seaward drift of kokanee or little redfish from Redfish Lake; (4) they were planted; (5) they were wanderers from other streams or lakes. Hauck believed explanations (2) and (3) were the most plausible.

Hauck's third explanation seems likely in view of information obtained in recent years. Lakes at the headwaters of the Salmon River that formerly contained sockeye salmon also contained nonanadromous forms commonly referred to as kokanee (*Oncorhynchus nerka*) and residual sockeye salmon (see discussion by Ricker, 1938, 1940, and 1959). Kokanee have been planted in some of the lakes in past years, but the nonanadromous forms were observed by Evermann during his 1894 and 1895 visits to the lakes. Locke (1929) reported kokanee or residual sockeye salmon in Redfish and Alturas lakes at a time when sea-run sockeye salmon could not get upstream past Sunbeam Dam. Fish found in Pettit and Yellowbelly Lakes, after chemical treatment in 1961 and 1962, appeared to be residual sockeye salmon. The fish were darker in coloration than the bright red kokanee and would have spawned later than the kokanee populations in Redfish and Alturas Lakes. We found no record of kokanee being planted in either Pettit or Yellowbelly Lakes.

Ricker (1959) and Foerster (1947) reported instances in which kokanee had returned to Cultus and Wenatchee Lakes after migrating to the ocean. Sockeye salmon (sea-run form) had not been observed at Alturas Lake for many years when in 1964, 45 fish which had evidently been to the ocean (based on their larger size) returned to the lake and were observed in the outlet and inlet streams of the lake. These sea-run fish spawned in the same inlet stream and at the same time (late August) as the kokanee; thus we believe they were kokanee which had gone to sea and returned. Redfish Lake sea-run sockeye salmon spawn on the lake shores during October.

Additional evidence in support of Hauck's third explanation was the large number of kokanee and/or residual sockeye salmon which emigrated from Redfish Lake as smolts during some years. Based on a likely survival from egg to smolt (less than 20%), more than half of the 1961 year class smolts were

TABLE 1.—*The number of adult sockeye salmon enumerated at the Redfish Lake Creek weir, and the dates of weir operation*

	Year												
Month	1954	1955[1]	1956[1]	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966
July	1			41	2	5	7	1	1	28	3		4
August	884			443	53	224	61	7	37	357	307	17	57
September	95			39	0	62	7	3	1	8	25	0	0
October	18									2			
TOTAL	998	4,361	1,381	523	55	290	75	11	39	395	335	17	61
Date of peak count	8/16			8/25	8/18	8/16	8/8	8/9	8/10	8/4	8/13	8/17	8/5, 10
Date trap installed	7/30			7/6	7/11	7/4	7/1	7/14	7/24	7/15	7/15	8/11	7/8
Date trap removed	10/29			9/10	9/8	9/29	9/23	9/11	9/12	10/21	10/8	9/17	9/20

[1] Daily count records for these two years were lost.

probably offspring of kokanee or residual stocks.

The stock of fish we have studied may differ from many sockeye stocks in that it may have originated recently from kokanee or residual sockeye salmon. If some upstream-migrating fish were able to pass Sunbeam Dam, it is not too unlikely that only a segment of the run passed successfully.

METHODS OF ENUMERATION

These studies were initiated in 1953 when personnel made repeated surveys of the Redfish Lake spawning grounds. In 1954 a temporary weir was installed in Redfish Lake Creek for the enumeration of adult sockeye. A permanent two-way weir (Craddock, 1958) was installed in the spring of 1955 and both smolts and adults were enumerated in 1955 and subsequent years by personnel of the Idaho Fish and Game Department and U. S. Bureau of Commercial Fisheries.

Adult sockeye salmon migrating upstream to Redfish Lake were captured in an adult trap in the center of the weir, and then counted out of the trap over a counting board except for those sampled for sex and length.

Downstream migrants were captured in inclined plane traps which strained all of the flow. The traps were checked periodically and fish removed as necessary. Fish were counted individually when small numbers were caught, but when large numbers were captured the entire catch was weighed and samples were taken to determine the number per pound and total catch. Random samples of 10–20 fish were measured and weighed alive each day and scales removed for age determination. The numbers of fish sampled for length-age determination ranged from 236 to 739 fish annually.

RETURNS OF ADULT SALMON TO REDFISH LAKE

Adult sockeye salmon destined for Redfish Lake comprised only a small part of the sockeye run entering the Columbia River each year. Only once since 1954 has the count at the Redfish Lake Creek weir (Table 1) amounted to more than one percent of the run entering the Columbia River.

Sockeye salmon enter the Columbia River primarily during June and July and pass Bonneville Dam during late June and July. Usually the first fish appeared at the weir after the middle of July and most of the run was passed during August (Table 1). Approximately 10% of the run passed the weir during early September. Spawning took place on the beach areas of the lake during October with the peak of activity about the middle of the month.

SIZE AND AGE OF ADULTS

Fork length of most sockeye salmon measured at the Redfish Lake Creek weir during the period 1953–65 ranged from 19.0 to 25.0 inches (483 to 635 cm) (Table 2). The mean length of females was approximately 21.5 inches (546 cm) and males averaged 22.7 inches (577 cm). The longer length of the males was, in part, caused by the elongation of upper and lower jaws associated with sexual maturation.

Redfish Lake sockeye salmon usually spent two years at sea and returned in their fourth or fifth year of life, depending on the number of years spent in the lake prior to seaward migration. A sample of 24 Redfish Lake sockeye salmon collected in 1953 (age determined from otoliths by Kenneth Mosher, pers. comm., 1953) had the same age-length relationship as upper Columbia River sockeye salmon studied by Craddock and Major (unpublished data). Fish smaller than 18 inches (457 cm) fork length had usually spent only one winter at sea (".1," age designation as suggested by Koo, 1962) while those longer than 18 inches had spent two or three winters at sea. Of the 24 otoliths examined by Mosher, 21 of the fish had spent two winters at sea (.2) and ranged in length from 20.2 (513 cm) to 24.7 inches (627 cm), 2 had spent three winters at sea (.3) and were both 23.5 inches (597 cm) in length, and 1 had spent one winter at sea (.1) and was 17.5 inches (445 cm) long. Most of the fish collected at the weir during the period 1953–1965 were 20–24 inches (508–609 cm) in length and had presumably spent 2 winters at sea (Table 2).

TABLE 2.—*Length-frequency distribution of adult sockeye salmon sampled at the Redfish Lake Creek weir 1953–1965*

Fork length (millimeters)	Males	Females
431–444		1
445–456	1	
457–469	1	
470–482	1	1
483–494	1	7
495–507	2	12
508–520	8	29
521–532	16	59
533–545	28	106
546–558	47	118
559–571	80	76
572–583	107	44
584–596	88	20
597–609	47	4
610–621	31	1
622–634	8	
635–644	9	
645–660	1	
TOTALS	476	478

The ratio of males to females in the spawning run enumerated at the Redfish Lake Creek weir was virtually 1 : 1 for all fish sampled during the years 1953–65 (Table 2). The nearly even sex ratio and predominance of the .2-fish in the Redfish Lake spawning escapement is similar to the Lake Wenatchee portion of the Columbia River sockeye salmon escapement and unlike the Lake Osoyoos escapement. Returning adults which have spent only one winter (.1) at sea have comprised more than half the Lake Osoyoos (Okanogan River) escapement in some years because of the selectivity of the commercial fishery for larger fish (Major and Craddock, 1962). A high percentage (1953–59 mean, 63%) of the .1 fish were males.

EGG DEPOSITION

Potential egg deposition (Table 3) was estimated from the total number of females counted over the weir each year and the average fecundity of upper Columbia River .2 sockeye salmon as determined by Major and Craddock (1962). We assumed that the

TABLE 3.—*The number of adult sockeye salmon counted at the Redfish Lake Creek weir, female spawners estimated egg deposition, smolts produced, fork length of yearling smolts, and percentage survival from egg to smolt*

Year class	Adults counted	Female spawners	Estimated egg deposition[1]	Number of smolts			Smolt length	Percentage survival
				Age I	Age II	Total		
1953					25,023			
1954	998	434	1,258,600	13,006	26,065	39,071	67.4	3.10
1955	4,361	1,999	5,797,100	38,935	40,139	79,074	76.7	1.36
1956	1,381	595	1,725,500	861	9,854	10,715	70.7	0.62
1957	523	275	797,500	3,146	1,442	4,588	87,7	0.58
1958	55	25	72,500	691	626	1,317	117.4	1.82
1959	290	130	377,000	20,974	1,978	22,952	105.4	6.09
1960	75	34	98,600	21,022	466	21,488	102.5	21.79
1961	11	6	17,400	22.854	2,175	25,029	93.3	143.84
1962	39	18	52,200	4,317	10,222	14,539	82.1	27.85
1963	395	202	585,800	8,778	3,627	12,405	87.5	2.12
1964	335	192	556,800	11,873			100.2	

[1] Average egg content per female used was 2,900 from Major and Craddock (1962).

fecundity of Redfish Lake sockeye was similar to that of upper Columbia River fish, that there was negligible year to year variation in the age-fecundity relationship, that virtually all eggs were deposited, and that all females were .2-fish. We did not verify the validity of the first two assumptions. The latter two assumptions appear to be reasonable based on the length frequency distribution of female fish sampled at the weir (Table 2) and examination of spent spawners.

SEASONAL MIGRATION OF JUVENILE SOCKEYE

Seaward migrant sockeye salmon departed from Redfish Lake from late April through May (Figure 2). The dates when largest numbers of fish left the lake ranged from 3 to 18 May for the years 1955–1966. In most years, a majority of the fish migrated during the first three weeks of May. Hartman, Heard, and Drucker (1967) studied the timing of smolt migrations for a number of Alaskan and British Columbia stocks and found a kindred relationship between latitude and timing. In order for the Redfish Lake stock (location at about 45° north latitude) to fit Hartman et al.'s relationship the timing of the smolt migration would have to have been in late March or early April rather than May.

Data on water temperature and stream flow were obtained each year, after 1957, to determine if these factors were related to the seasonal timing of the migration. During most years the migration of sockeye salmon juveniles from the lake coincided with increases in maximum stream temperatures at the weir and stream flows (Figure 2). (Maximum daily temperatures were compared with migration of smolts rather than minimum or mean temperature because we believed the maximum might better portray the attainment of a threshold temperature if one existed. Mean temperature could probably have been used with similar results.) But exceptions occurred, indicating that the seasonal timing of migration was not controlled primarily by stream temperature and flow.

Although migration occurred as maximum stream weir temperatures were increasing and ranged from 38 to 50 F, the warming of the waters in the stream during April and early May usually occurred in the ½ mile between the lake and weir. Water temperatures at the outlet of the lake were approximately 39 F when an ice cover was present. On warm sunny days the stream temperature, at the weir, was as much as 10 F warmer than at the outlet. Migrants leaving the lake when an ice cover was present (as in 1961, 1962, 1963, 1964, and 1966, Figure 2) were not influenced by the warmer water temperatures in the stream until after they had left the lake and proceeded some distance downstream. On cold, overcast days, the stream temperatures did not exceed 39 to 41 F, but migration continued uninterrupted (such as on 17 May 1965; 2 May 1959; 6 and 12 May 1958).

Burgner (1962) concluded that climate was the most influential factor in timing the seasonal migration of sockeye salmon smolts from the Wood River lakes, Alaska. The start of seaward migration was delayed until lake outlet temperatures reached 38–39 F, following breakup of the ice cover on the lakes. Burgner cited other authors who reported that seaward migration of sockeye salmon smolts followed breakup of the lake ice cover and increased lake outlet temperatures of 39 F or higher.

At Redfish Lake, the maximum outlet stream temperature always exceeded 38–39 F during the period smolts were migrating from the lake. But migration did not always begin as soon as outlet temperatures reach 38–40 F (see years 1960, 1964, and 1965, Figure 2), nor was it delayed until the breakup of ice cover on the lake (years 1961, 1962, 1963, 1964, and 1966).

Migration of smolts usually coincided with increasing flows, but there were years, such as the 1961 peak, when a large number of fish migrated before any increase in stream flow had occurred (Figure 2). Daily catches of seaward migrants increased to a large number in both 1963 and 1966 before any increase in flows occurred.

The stimulus or stimuli which served as a releaser for the migration of smolts from Redfish Lake is unclear to us. There was no consistent relationship between timing of the

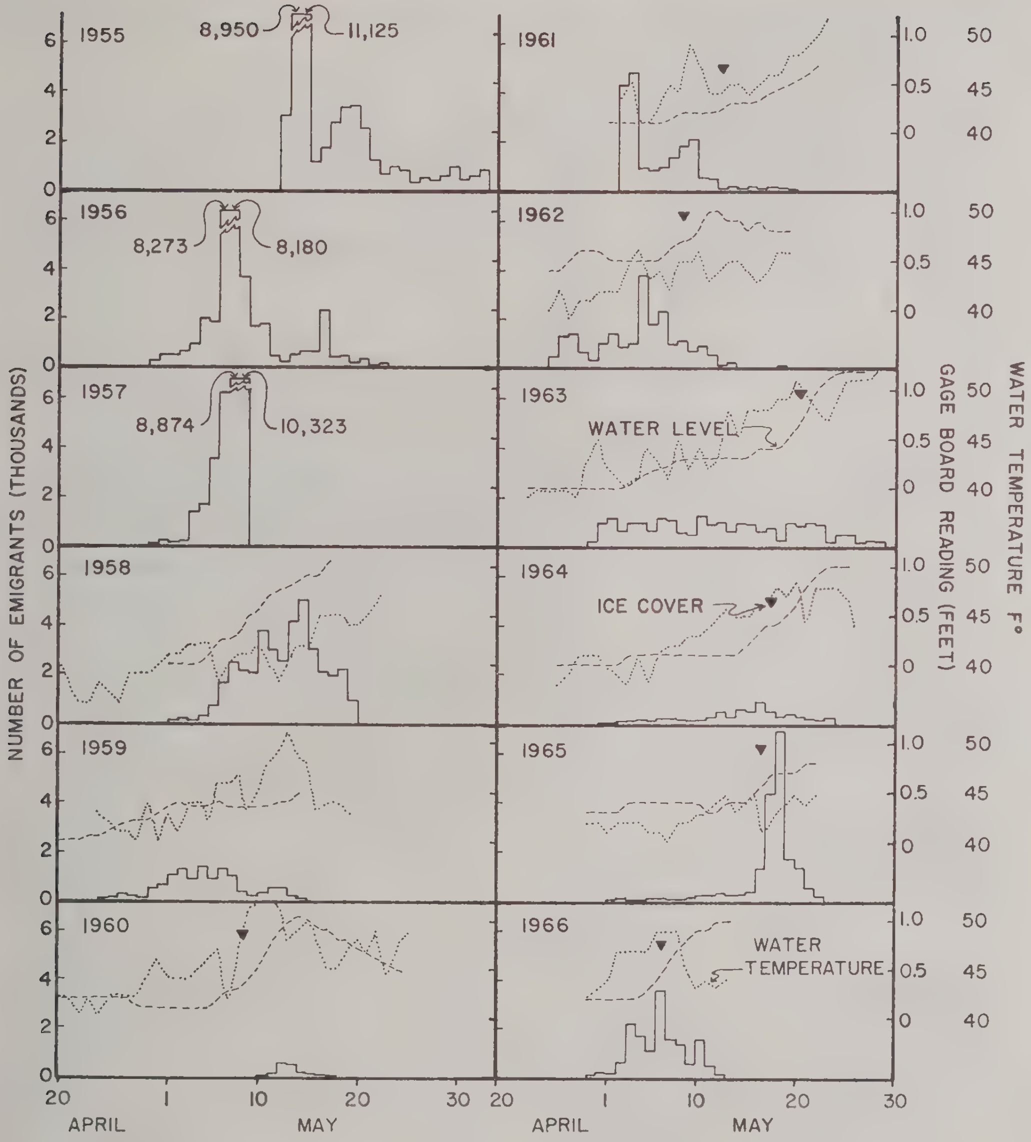

Figure 2.—Daily counts of sockeye salmon smolts at the Redfish Lake Creek weir as related to stream flow (gage board reading), water temperature at weir, and date ice cover left lake.

migration, lake ice cover, temperature or flow of the outlet stream. Through the process of elimination, we have concluded photoperiod may play an important role as a releaser for many of the behavioral actions and physiological processes associated with seaward migration, but this is a speculation on our part. Hartman et al. (1967), after their analysis of possible factors affecting smolt migration timing, turned to photoperiodism as the overriding stimulus or releaser.

Both behavioral and physiological changes take place during the transformation from parr to smolt. Physiological changes in salmonids, such as ability to adapt to sea-

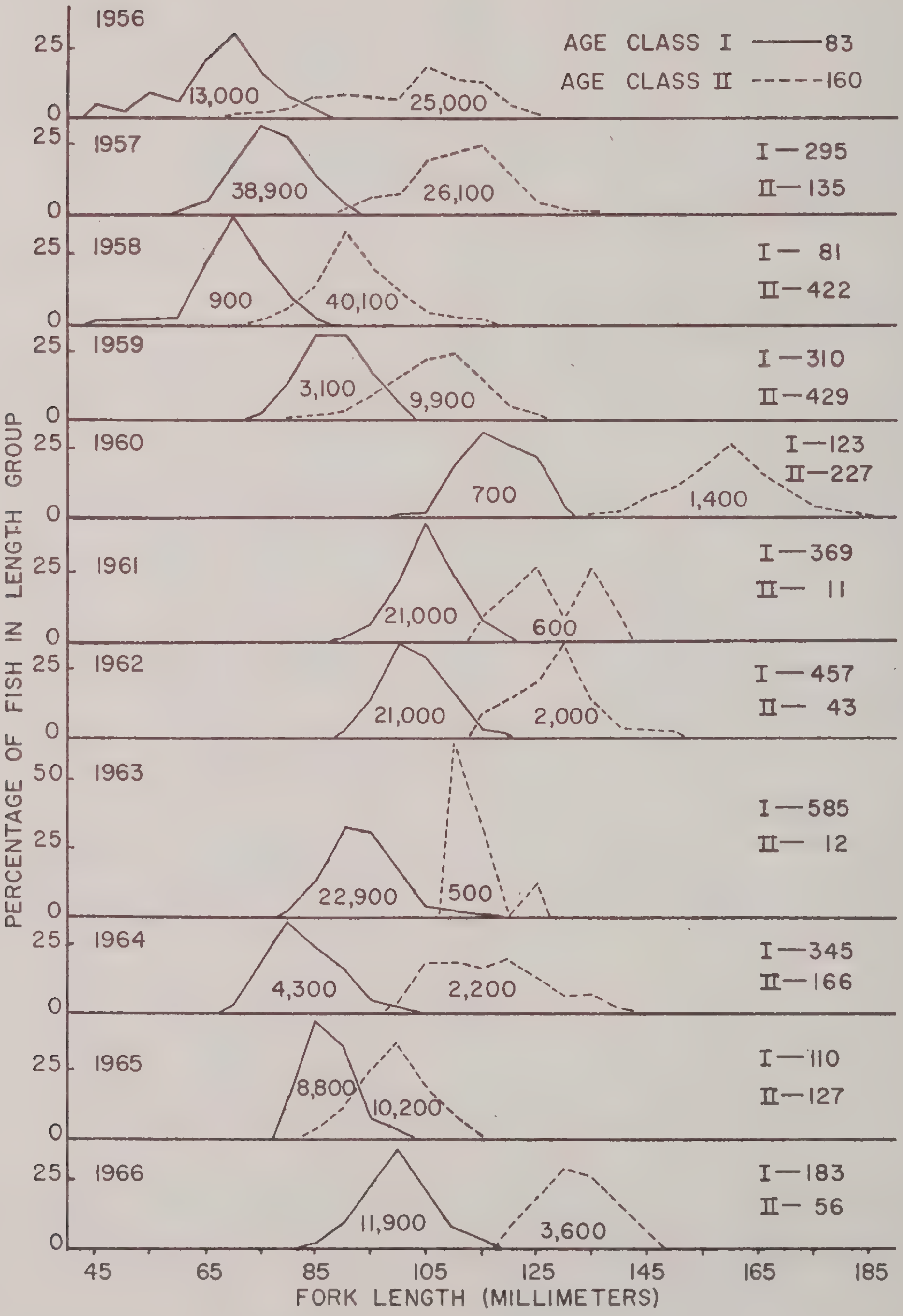

FIGURE 3.—Length-frequency distribution and estimated number of sockeye salmon smolts passing the Redfish Lake Creek weir. Number in sample listed opposite age class designation.

TABLE 4.—*Diel migration pattern of sockeye smolts past Redfish Lake Creek weir, 1956–1962*

Year	Hour							
	0600–1200		1200–1800		1800–2400		0000–0600	
	N	%	*N*	%	*N*	%	*N*	%
1956	0	0.0	210	0.7	22,165	76.2	6,732	23.1
1957	393	1.3	137	0.5	23,759	78.2	6,106	20.1
1958	0	0.0	842	2.8	23,133	76.3	6,341	20.9
1961	134	0.7	185	0.9	16,267	81.4	3,401	17.0
1962	15	0.1	2,591	11.6	14,551	65.1	5,201	23.3
Total	542	0.4	3,965	3.0	99,875	75.6	27,781	21.0

water, may begin to occur many months before seaward migration takes place (Conte and Wagner, 1965 and Conte, Wagner, Fessler, and Grose, 1966). Photoperiod may be the environmental cue (if one is needed) that initiates the physiological changes and could be the releaser for migration. But the seasonal change in day length does not appear to be the only factor regulating the smolt transformation. Both juvenile sockeye salmon and steelhead trout (*Salmo gairdnerii*) may pass through one or two seasonal photoperiod cycles without becoming smolts. The age of the fish when smolt transformation takes place appears to be regulated partially by growth, especially for sockeye salmon and steelhead trout. Thus we speculate that photoperiod may be the releaser for the parr-smolt transformation but only if the fish have attained a threshold size.

DIEL MIGRATION OF JUVENILE SOCKEYE

The main downstream movement of fish did not start until shortly after dark, peaked about 2230 or 2300 hr and then decreased. Large schools of smolts were not observed leaving the lake, but were often seen entering the weir pond just at dusk. Seventy-six percent of the migrants were captured between 1800 and 2400 hr, 21% between 2400 and 0600 hr and only 3% in the combined period of 0600 to 1800 hr (Table 4). Young sockeye migrants moved during hours of darkness. We also observed that the smolts spilled into the traps in groups rather than singly, indicating schooling behavior after dark.

NUMBER OF JUVENILE MIGRANTS

The number (estimated or actual count) of juvenile sockeye salmon migrating from Redfish Lake ranged from 2,133 to 65,000 during the years 1955–1966 (Table 5). Complete or nearly complete counts of migrants were obtained in 9 of the 12 years of weir operation. In 1955 and 1961 trapping was not initiated until after the migration had begun. In 1957, trapping had to be discontinued after the day of largest catch because of high stream flows. In other years trapping was discontinued before the entire migration had been counted but we believe only a small part of the run was missed based on the trend of daily catches (Figure 2). Estimates of the total number of migrants were made by examination of the histogram of daily catches (Figure 2) and subjective extrapolation of the daily catch curve for the part of the run missed.

TABLE 5.—*The number of sockeye salmon smolts counted at the Redfish Lake Creek weir and the estimated total migration*

Year	Days weir operated	Number counted	Estimated total number of migrants[1]
1955	24	48,895	54,000
1956	35	38,029	38,029
1957	19	32,857	65,000
1958	20	38,555	41,000
1959	23	12,324	13,000
1960	49	2,133	2,133
1961	20	19,987	21,600
1962	25	22,358	23,000
1963	36	23,320	23,320
1964	29	6,492	6,492
1965	24	18,479	19,000
1966	14	15,159	15,500

[1] See text for explanation of method of estimating total number of migrants.

AGE AND LENGTH OF JUVENILE MIGRANTS

Sockeye salmon migrated from Redfish Lake at the beginning of their second or third summer of life. The percentages of the two age classes in the migration each year varied from 2 to 98% (Table 6).

Growth of sockeye salmon in Redfish Lake varied annually (Figure 3), appearing to be related at least partially to density of fish in the lake (Figure 4). Fish of both age classes which migrated in 1960 were the largest observed (Figure 3) and the number of migrants counted that spring was the smallest in 12 years of sampling. Yearlings (fish having spent one growing season and winter in lake and having only one annulus) migrating in 1956, 1957, and 1958 were the

TABLE 6.—*Number of sockeye salmon and percentage of each age class in the migration from Redfish Lake, 1955 to 1966*

Year	Total migrants	Percentage age class I	Percentage age class II	Number of age class I	Number of age class II
1955	54,000				
1956	38,029	34.2	65.8	13,006	25,023
1957	65,000	59.9	40.1	38,935	26,065
1958	41,000	2.1	97.9	861	40,139
1959	13,000	24.2	75.8	3,146	9,854
1960	2,133	32.4	67.6	691	1,442
1961	21,600	97.1	2.9	20,974	626
1962	23,000	91.4	8.6	21,022	1,978
1963	23,320	98.0	2.0	22,854	466
1964	6,492	66.5	33.5	4,317	2,175
1965	19,000	46.2	53.8	8,778	10,222
1966	15,500	76.6	23.4	11,873	3,627

smallest measured and were more abundant than in other years.

In the number-length of migrants relationship presented in Figure 4 we used the number of all migrants (age I and II) as a measure of density of fish in the lake. The correlation between number of migrants and length of yearling migrants was not high ($r = .64$), confidence interval at .95 level-.05, -.88). (In an attempt to provide some statistical measure of the relationship in Figure 4 and others presented later we have computed correlation coefficients, r, and coefficients of determination, r^2. The correlation was not high for any of the relationships examined. The precision of the r values was poor because of the small (from a statistical standpoint) sample size (11 years of data) and the low correlation.) We could say that 41% ($r^2 = .41$) of the variation in length of yearling migrants was from variation in number of migrants, however, the reliability of such a statement is poor because of the wide confidence interval of r.

A higher degree of correlation between length of migrants and density of fish may have been found if we had a better measure of fish density during the yearlings growing period in the lake. Yearlings which did not migrate but remained in the lake another year were not included in Figure 4. By including the yearlings which survived and migrated a year later the relationship was not changed materially from that portrayed in Figure 4. We did not have a reliable index of kokanee or residual sockeye abundance in the lake but believe large numbers were present in some years.

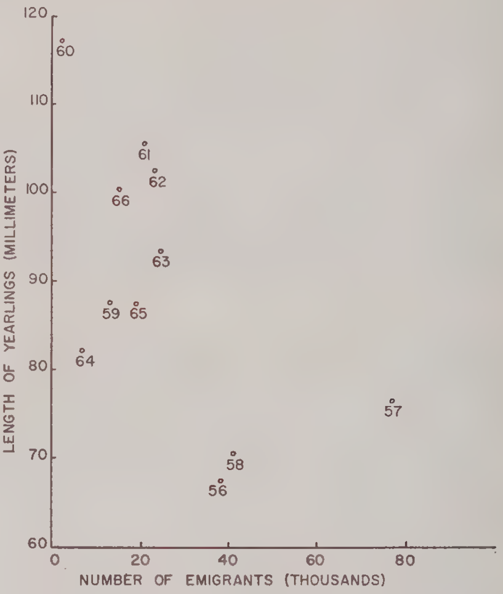

FIGURE 4.—Estimated number of sockeye salmon smolts migrating from Redfish Lake and the length of yearling migrants. Year of migration listed below each point.

We did not find any tendency for one of the age classes to migrate during a particular part of the migration period, as was found by Nelson (1959) and Burgner (1962). During the six years when large numbers of both age classes were present in the migration the proportion of age class I fish decreased as the migration proceeded in three years while in the other three years the proportion increased or remained unchanged.

There was a relationship between the age at which juvenile sockeye salmon migrated from Redfish Lake and their growth during their first summer in the lake (Figure 5). When the mean fork length of yearling migrants was less than 80 mm (millimeters), less than 50% of the eventual migrants of a year class (the year the parents spawned) left the lake as yearlings. As the mean length of a year class approached 100 mm, more than 90% of the fish migrated as yearlings. Migrants of the 1958 year class were exceptions, as yearlings of this group were the largest observed in 12 years but only 52.5% migrated as yearlings. The 1958 year class may or may not be representative of a growth-

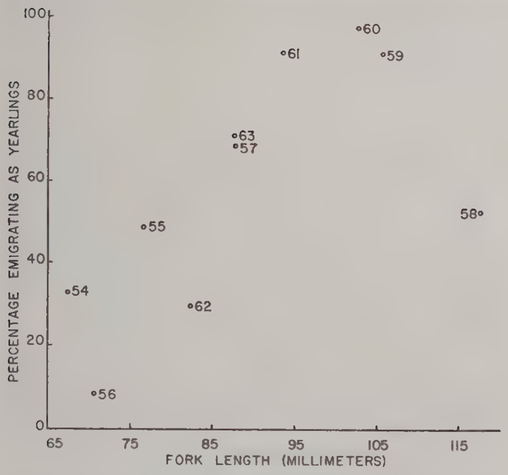

FIGURE 5.—Length of yearling sockeye salmon smolts migrating from Redfish Lake and percentage of year class migrating as yearlings. Year class listed next to each point.

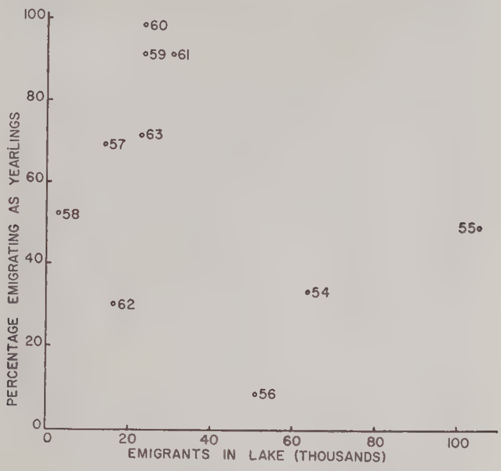

FIGURE 6.—Number of eventual sockeye salmon migrants in Redfish Lake during first summer of rearing for fish of each year class and percentage of year class migrating the following spring as yearlings. Year class listed near each point.

age at migration relationship of fish in the lake. The number of 1958 year class smolts was the smallest (1,317 fish) observed during the study. A high percentage of the year class could have remained in the lake a second summer merely by one or two schools of age I fish failing to find the outlet. On the other hand, the 1958 year class may be a case of seaward migration being delayed when growth is good and density low, as discussed by Rounsefell (1958).

The correlation coefficient, r, for the data in Figure 5 was 0.65, with $r^2 = 0.42$. If the data of the 1958 year class were not included r would be 0.89 and r^2 0.79. Thus without the 1958 data, or up to a migrant length of 105 mm, a high percentage of the variation in percentage of a year class which migrated as yearlings could be explained by variation in growth (length) of yearlings.

The percentage of a year class migrating as yearlings was not closely correlated with the total number of eventual migrants (all smolts of a year class plus age II smolts of previous year class) in the lake during the first summer of life of the yearling migrants (Figure 6). The number of eventual migrants present in the lake during each summer was our best index to possible density-related growth compensation. Only 13% ($r^2 = 0.1317$) of the variability in percentage of a year class which migrated as yearlings could be "explained" by variation in the measurable lake population (number of migrants). If the percentage of a year class which migrated as yearlings was regulated by length of yearlings (Figure 5) and growth controlled (at least partially) by population density (Figure 4) then we might expect a correlation between population density and percentage migrating as yearlings (Figure 6). Since r^2, for the data in Figure 6, was only 0.1317 we must conclude that the number of eventual migrants in the lake was not an accurate index of population density or that growth was not affected by population density. We subscribe to the former alternative.

We have concluded that (1) growth of juvenile sockeye salmon in Redfish Lake was inversely related to population density, and (2) the age at which a young salmon migrated to the sea was primarily dependent upon its growth during the first summer of life. If population density was low and growth good the young salmon would be likely to migrate after one year of lake rearing. If growth was unusually good, such as for the 1958 year class, migration may be delayed. If growth was slow, due to high population density, for example, the chances were increased the fish would remain in the lake a second year.

Our conclusions regarding the sockeye salmon population at Redfish Lake are in partial but not full agreement with observations of others in Alaska and British Columbia. Burgner (1962) concluded that "differences between lakes in degree of competition between fry for food were apparently a major source of differences in growth attained." Nelson (1959) concluded that an increase in size of smolts at Bare Lake, Alaska did not result in an increased percentage of younger smolts in the seaward migrations. In addition he observed that when large numbers of migrants left the lake younger fish comprised a higher percentage of the migrants perhaps from population pressures. Rounsefell (1958) concluded that weight of individual smolts was inversely related to population density at Cultus Lake but not at Karluk Lake, and proposed that migration was induced both by size and density of young. At a high density the fish might leave at an earlier age because of population pressure.

Meehan (1966) concluded that size of smolts from two Alaskan lakes was inversely related to the potential density of fry in the lakes. In addition he stated that "the length of time of freshwater residence of sockeye . . . appear to be correlated negatively with density of fry . . ." On the basis of Meehan's conclusions, low fry densities would have produced larger smolts and a smaller proportion of yearling migrants and smaller smolts and more yearling migrants with high densities. At Redfish Lake we found that size of yearling smolts and proportion of yearling migrants was largest when fry density was low, as indicated from potential egg deposition (except for 1958 year class). When fry density was high both size of smolts and the proportion of yearlings in the migration were smaller (Table 3).

Based on the data presented in Figure 5, we could expect less than 50% of the emigrants of a year class to leave Redfish Lake as yearlings if the yearlings were less than about 85 mm fork length. If the yearlings were larger than 85 mm (up to 105–110 mm) we could expect more than 50% to migrate as yearlings.

SURVIVAL IN THE LAKE

The survival of juvenile sockeye in Redfish Lake from potential egg deposition to smolt migration was unusually variable (Table 3). For the year classes in which less than 100,000 eggs were deposited the smolts enumerated comprised about 2 to 144% of the potential egg deposition.

The survival percentage of 144 for the 1961 year class was evidence that sockeye salmon smolts from Redfish Lake may originate from kokanee and/or residual sockeye salmon as well as the usual sea-run form of adult. There were more 1961 year class smolts enumerated than sea-run sockeye eggs available for deposition.

The smolts which did not originate from sockeye salmon may have been: (1) offspring of kokanee which spawned in a tributary to Redfish Lake, (2) kokanee which were released into Redfish Lake as young of the year fish in 1962, and (3) offspring from kokanee and/or residual sockeye salmon which spawned on the shoreline of the lake. Each year Fishhook Creek, the only Redfish Lake tributary used for spawning, was observed to determine if spawning kokanee were present. In 1961 no fish were observed. During the years of study, we did not observe kokanee and/or residual sockeye salmon spawning on the shoreline spawning areas in the lake, but our observations were limited.

The only release of kokanee into Redfish Lake, during the years of study, was made during July of 1962 when 42,900 kokanee fingerlings of the 1961 year class were released into the lake. These kokanee could have migrated from the lake during the spring of 1963 as yearlings along with the 1961 year class sockeye salmon offspring. The recovery of only four marked kokanee (6,825 marked before release with a right ventral fin-clip) among 6,209 smolts examined in the spring of 1963 was an indication that few of the planted kokanee migrated from the lake. The four marked kokanee had an average length of 78.5 mm while the

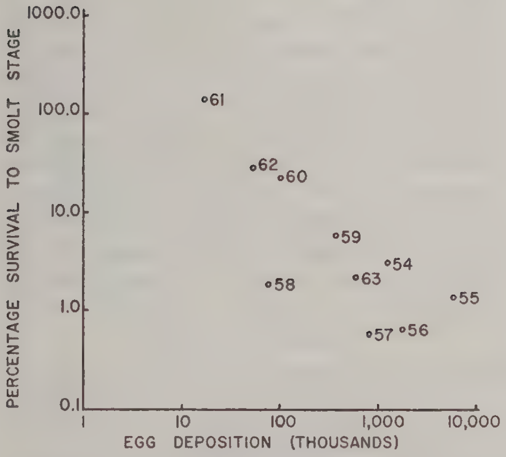

FIGURE 7.—Estimated egg deposition by sockeye salmon spawners in Redfish Lake and percentage survival of eggs to smolt stage. Year class listed near each point.

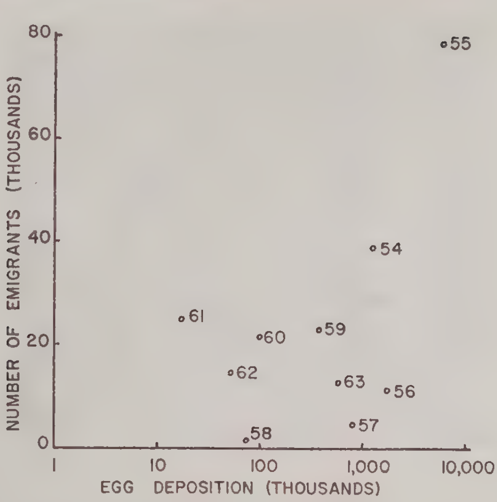

FIGURE 8.—Estimated egg deposition by sockeye salmon spawners in Redfish Lake and number of smolts leaving lake. Year class listed near each point.

average length of the yearling smolts was 93.3 mm. The marked kokanee may have grown slower and had poorer survival than the unmarked kokanee. No marked kokanee were found in the 1964 smolt migration.

The 1960 and 1962 year class percentage survivals were also high (Table 3), but perhaps not unreasonable since the egg deposition was small and we might expect survival to be inversely related to population density in the lake. Meehan (1966) concluded that freshwater survival (2.0 to 8.5% at Kitoi Lake) was inversely related to the potential number of fingerlings in the lakes he studied. When we plotted the percentage survival against egg deposition in Redfish Lake (Figure 7) there appeared to be an inverse relationship, but the coefficient of determination, r^2, was only 0.084 indicating that only 8% of the variation in percentage survival could be "explained" by the variation in egg deposition. If the points representing the year classes 1960, 1961, and 1962 are removed from Figure 7 it is more obvious that percentage survival was similar over a 100-fold increase in egg deposition.

Although the largest numbers of smolts were from the brood years of largest egg deposition there was little relationship between egg deposition and numbers of smolts produced (Figure 8). For egg depositions in the range of 100,000 to more than one million the number of smolts produced averaged about 20,000 fish. Burgner (1962) concluded that "conditions for survival were more important than abundance of spawners in determining abundance of smolts" in the Wood River Lakes. The production of smolts from a small British Columbia sockeye population was similar to that at Redfish Lake; 11,000 to 20,000 smolts from egg depositions of 300,000 to 2,000,000 (cited by Burgner).

Freshwater survival of juvenile sockeye at Redfish Lake was similar to that observed by Foerster (1945, 1955), Barnaby (1944), Nelson (1959) and Meehan (1966) except for the 1961 year class and perhaps the 1960 and 1962 year classes.

SMOLT TO ADULT SURVIVAL

The survival of smolts from migration to returning adults counted at the weir has ranged from 0.14 to 1.83% (Table 7). The number of adults returning to the weir appeared to be regulated somewhat by the commercial fishery harvest in the lower Columbia River. The percentage survival of smolts which left the lake during the years 1956–1959 was much less than those which left in subsequent years. Smolts which left the

TABLE 7.—*The number of smolts which emigrated from Redfish Lake, year of migration, adults returning two years later to the weir, percentage survival, and percentage of sockeye run harvested by the Columbia River commercial fishery*

Year of migration	Migrating smolts	Returning adults	Percentage	
			Survival[1]	Harvest[2]
1955	54,000	523	0.97	44.0
1956	38,029	55	0.14	62.9
1957	65,000	290	0.45	68.3
1958	41,000	75	0.18	66.4
1959	13,000	11	0.08	69.9
1960	2,133	39	1.83	37.0
1961	21,600	395	1.83	21.4
1962	23,000	335	1.46	19.8
1963	23,320	17	0.07	10.6
1964	6,492	61	0.94	2.5

[1] All adults assumed to have spent two years in ocean.

[2] Data from: The 1966 Status Report of the Columbia River Commercial Fisheries, Fish Commission of Oregon, Washington Department of Fisheries, 97 pp.

lake during the years 1956–1959 returned as adults during the years 1958–1961; a period when the commercial fishery was harvesting more than 60% of the sockeye salmon run. In subsequent years, the commercial fishery harvested a smaller percentage of the run. Since the commercial fishery was selective to larger fish and few of the Redfish Lake fish are small, the fishery may have taken a disproportionately large share of the fish destined for Redfish Lake. Additional information on the timing of the Redfish Lake salmon through the fishing area would have to be determined before any definite conclusions could be made.

Adequate scale samples were not available from all returning adult runs to assess the effect of smolt size and age on survival to adult. No special effort was made to collect scale samples because (1) some runs were too small to allow extensive handling, and (2) the many sources of mortality (irrigation diversions, dam and reservoir passage, commercial fishery) would likely confound the survival determinations. For the years when the smolt migration was composed largely of one age group (1958, 1961, 1962, and 1963) the survival rate was highest when the smolts were the largest. We have limited confidence in these findings because of the small number of observations and possible confounding mortality factors.

Smolt to adult survival rates for Redfish Lake sockeye salmon are less than the rates observed for other stocks of fish. Foerster (1945) reported survival rates averaging 9.9% for Cultus Lake fish, Barnaby (1944) reported an average 21.4% survival for Karluk Lake fish, and Nelson (1959) reported survivals of 3.26–7.89% for Bare Lake fish (returning adults include fish harvested in fisheries). The survival rates for Redfish Lake sockeye would not be as large as the rates for the stocks listed above even if increased by as much as three times to compensate for the commercial fishery harvest.

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THE SUBFAMILY TELLININAE IN THE WESTERN ATLANTIC THE GENERA TELLINA (Part II) AND TELLIDORA[1]

BY

Kenneth J. Boss

Subgenus **Eurytellina** *Fischer*

Peronaeoderma 'Poli' Stoliczka 1870, Cretaceous Fauna of Southern India, **3**: 116 (type species, *Tellina punicea* Born 1778, original designation), *non* Poli 1795, *nec* Mörch 1853.

Eurytellina Fischer 1887, Manuel de Conchyliologie, p. 1147 (type species, *Tellina punicea* Born 1778, monotypy).

Tellinota Iredale 1936, Rec. Aust. Mus., **19**(5): 281 (type species, *Tellinota roseola* Iredale 1936, original designation).

Description. Shell elongate-elliptical to subtrigonal, somewhat compressed and slightly inequilateral; posterior flexure to the right, weak, obsolete or absent; surface sculpture rather poorly developed; ligament posterior, more or less protuberant, and strong; lateral teeth of the left valve poorly developed with a weak, tubercle-like proximal anterior tooth and an obsolete distal posterior lateral tooth; in the right valve, the distal posterior tooth is often well developed and the proximal anterior is generally well developed and strong; pallial sinus rather flattened dorsally and extending far anteriorly, near to or contiguous with the anterior adductor; confluence of the pallial sinus with the pallial line extensive. Anterior internal rib extends from the umbonal region to the anterior adductor scar and is strong, especially in the left valve.

The group of *Eurytellina* forms a natural assemblage of species characterized by the right lateral dentition, the more or less elongate elliptical shape of the shell, the compression of the valves, the strength of the internal radial rib and the relatively smooth superficial sculpture on the anterior slope and disc of each valve. The group appears to be most highly developed within the Western Atlantic and Eastern Pacific regions and constitutes a large element of the fauna. It is, furthermore, represented in the Indo-Pacific region by such species as *Tellina albinella* Lamarck of South Australia.

In the Western Atlantic, *Eurytellina* is more or less restricted to the shallow subtropical and tropical seas although a single species extends north to Cape Hatteras. The central area of concentration of species is the Caribbean. Three species are found in the Brasilian fauna but none of these is endemic. In the Eastern Pacific, the group is represented by more species, which have developed since the appearance of the subgenus in the Oligocene and Lower Miocene of North America.

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[1] *Correction.* In Johnsonia no. 45 on pp. 268 and 271, Plates 141 and 142 are reversed. The plate caption on p. 268 applies to the plate on p. 271 and the plate caption on p. 271 applies to the plate on p. 268.

KEY TO THE SPECIES OF THE SUBGENUS *EURYTELLINA* IN THE WESTERN ATLANTIC

1. Posterior dorsal slope of the right valve with differentiated strong concentric sculpture 2
   Posterior dorsal slope sculpture on the right valve not differentiated, similar to the sculpture on the central disc 3

2. Shell with an orange-apricot colored periostracum; adult size larger than 20 mm. . . . . . . *nitens*
   Shell white to pellucid; very small in size (smaller than 15 mm. in adult) with a sharp posterior ridge in the right valve: left valve broadly tumid and convex . . . . . . *vespuciana*

3. Shell with numerous colored radial rays extending from the umbonal area to the periphery . . . . . . *guildingii*
   Shell unrayed or with one or two radial streaks extending anteriorly and posteriorly from the umbo but not extending to the periphery . . . 4

4. Shell sharply flexed to the right posteriorly; left valve broadly convex . . . . . . *lineata*
   Shell not flexed or only very weakly flexed to the right posteriorly . . . 5

5. Shell bright red or purple; pallial sinus usually touching the anterior adductor muscle scar . . . . . . *punicea*
   Shell not bright red or purple; pallial sinus usually free from the anterior adductor muscle scar 6

6. Shell high and subtrigonal in shape 7
   Shell elongate-subtrigonal in shape 8

7. Shell with regular widely spaced incised sulci . . . . . . *angulosa*
   Shell with sulci poorly incised and irregular . . . . . . *trinitatis*

8. Shell white or suffused with yellow or pink internally; lateral surface of anterior dorsal margin narrow; left valve weakly convex . . . *alternata*
   Shell pink; lateral surface of anterior dorsal margin wide; left valve flattened on the disc . . . . . . *tayloriana*

Tellina (Eurytellina) punicea *Born*

Plate 143, fig. 2; Plate 144, fig. 2; Plate 150, fig. 3

Tellina punicea Born 1778, Index Museum Caesarum Vindobinensis, p. 22; 1780, Index Mus. Caes. Vind., p. 33, pl. 2, fig. 8 (Patria ignota) [type locality, here restricted, Guayaguayare Beach, Trinidad; types not seen].

Tellina punicea Born. d'Orbigny 1853 [*in*] Sagra, Hist. L'Ile Cuba, Mollusques, **2:** 298 (*pars*).

Tellina (*Peronaeoderma*) *punicea* Born. H. and A. Adams 1856, Genera Recent Mollusca, **2:** 396.

Tellina (*Eurytellina*) *punicea* Born. Fischer 1887, Manuel de Conchyliologie, p. 1147.

Tellina (*Eurytellina*) *angulosa* 'Gmelin' Gardner 1928, United States Geol. Survey, Prof. Papers 142-e, p. 193, *non* Gmelin 1791.

Tellina (*Eurytellina*) *punicea* Born. Warmke and Abbott 1962, Caribbean Seashells, p. 195, pls. 4g and 40d.

Description. Shell extending to 45 mm. (about 1¾ inches) in length and to 28 mm. (about 1 inch) in height, elongate, nearly equilateral, moderately inflated, with the right valve more convex and with an extremely weak posterior flexure to the right. Umbos just posterior to the middle, rounded, and rather inconspicuous. Anterior margin broadly and smoothly rounded; ventral margin straight or slightly convex, rising gently posteriorly; anterior and posterior dorsal margins usually subequal in length and gently sloping; posterior margin short, straight or slightly convex, giving a somewhat truncated appearance to the outline of the shell. Sculpture consisting of weakly incised concentric sulci separated by broad bands; these concentric bands are nearly equal in breadth in opposite valves. Ligament dark brown and somewhat sunken in a broad but shallow escutcheon; lunule narrow, shallow and long. Calcareous element of the ligament subtended by a rather strongly developed nymphal callosity in the right valve. Hinge line moderately developed. In the left valve, the cardinal complex consists of an interior thin, bifid tooth with subequal lobes and of a posterior, widely divergent, thin, laminate tooth; proximally anterior to the cardinal complex is a well developed but small lateral tooth. In the right valve, the cardinal complex consists of a posterior strong, skewed, deltoid, bifid tooth with the posterior lobe the larger and of an anterior strong, thickened, subdeltoid, laminate tooth; anterior lateral tooth well developed and proximal to the laminate cardinal tooth; posterior lateral tooth distal to the cardinal complex, strong and well developed. A rib extends from the umbonal region to the anterior adductor muscle. Muscle scars well impressed. Anterior adductor scar a little narrower and longer but not much higher than the posterior adductor scar. Pallial sinus equal in both valves, flattened

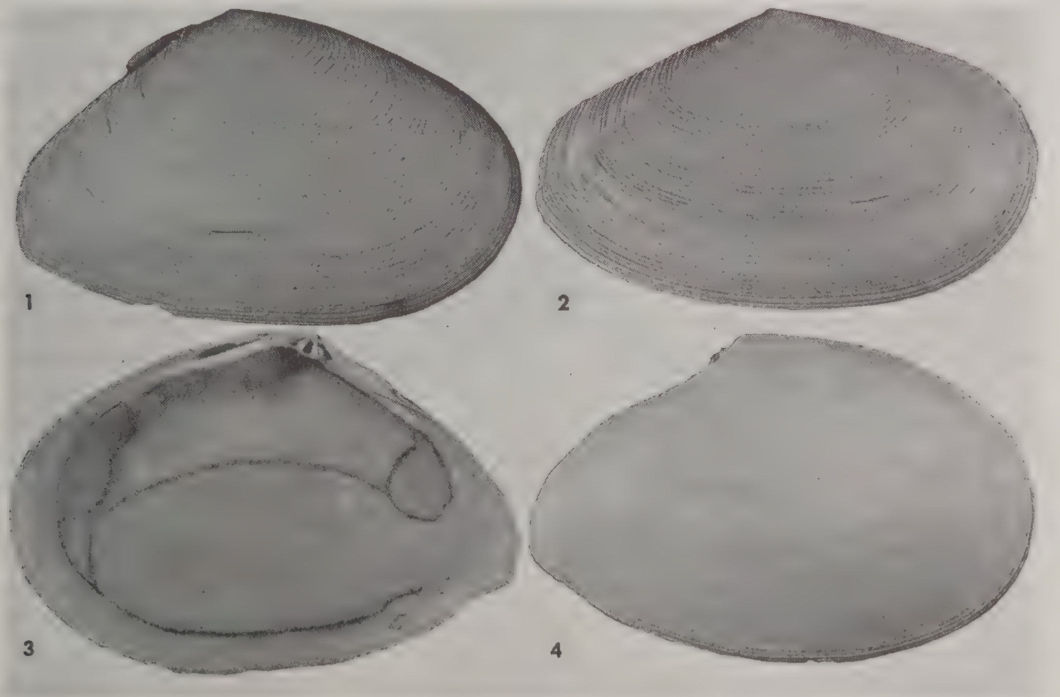

Plate 143. Fig. 1. *Tellina angulosa* Gmelin, external view of the right valve, St. Croix, Virgin Islands, MCZ 236382 (about 1.6x) [L=40 mm.]. Fig. 2. *Tellina punicea* Born, external view of the right valve, Punta Guanajibo, Puerto Rico, MCZ 236395 (about 2.4x) [L=31 mm.]. Figs. 3–4. *Tellina lineata* Turton. Fig. 3. Internal view of the right valve (about 2.5x) [L=30 mm.]. Fig. 4. External view of the right valve, Marco, Florida, MCZ 166044 (about 3.7x) [L=21 mm.].

above and extending to and most often coalescing with the anterior adductor scar. The pallial sinus falls abruptly and straight to the pallial line and is confluent with it for most of its length. Externally, the shell is alternately and irregularly banded with white and dark red or purple. Internally the shining surface is generally a deep red or purple with a white periphery and with some suffusion of white especially in the region of the anterior rib and umbonal cavity.

length	height	width	
44.5 mm.	27.5 mm.	11.5 mm.	Gulf of Paria, Trinidad
42.5	27.0	10.5	Waunta Haulover, Nicaragua
40.0	25.0	9.2	Belize, British Honduras
38.9	24.6	10.3	Waunta Haulover, Nicaragua
38.5	22.5	8.5	Punta Guanajibo, Puerto Rico
27.4	16.6	5.3	Cartagena, Colombia
23.0	17.0	4.5	Puerto Plata, Santo Domingo
17.2	10.8	3.3	Cartagena, Colombia

Remarks. A great deal of confusion has reigned in the problem of recognizing this species. The name itself was originally introduced by Born in his Index in the 1778 edition: at that time no figure or locality was given. The description makes a considerable point of the coloration of the shell as well as the concentric striations and the growth lines. In 1780, a plate constituting the type figure accompanied the text, but unfortunately a view of the internal surface of either valve is not given; however, the shape of the shell, specifically its outline, as well as the external sculpture give a good representation of what today is considered *punicea.* A further difficulty lies in the fact that no type locality was given and subsequent workers, deciding that the species was West Indian, were not wont to restrict the locality. Since the species is very closely allied to *Tellina simulans* Adams of the Eastern Pacific, the difficulties encountered in the discussion of these species have been considerable.

Coloration is one of the major keys for recognizing *Tellina punicea;* indeed, Born's descriptive 'dunkel-rot' succinctly identifies most specimens. However, individuals in any population show considerable variation in degrees of purple or redness. As a matter of fact, a cline exists through the north-south range of the species where the most intensely red individuals are to be found in the Caribbean and where the proportions of deep redness decreases towards the south in Brasil. Another characteristic, employed to separate this species from others closely related to it or confused with it, is the fact that the pallial sinus extends to, touches, and even coalesces with the anterior adductor muscle scar. But even this character is not infallible, since in some lots, in one valve of a specimen, the sinus may not quite touch the anterior muscle scar but be connected to it by means of a short linear scar. Nevertheless, there can be no doubt about *punicea* when complete specimens taken in a series are examined. The coalescence of the pallial sinus with the muscle scar, the elongate shape of the shell, the irregularly concentric sculpture, the concentric banding of coloration of the interior best characterize the species.

Allometric differences also occur. Younger specimens, in general, have a slightly different proportion than the adult or larger specimens. The shells are lower and appear more elongate; the posterior rise or arcuation of the ventral margin is more noticeable and the posterior dorsal margin tends to be markedly convex. In addition to the previously mentioned cline in coloration, some clinal variation occurs with respect to the

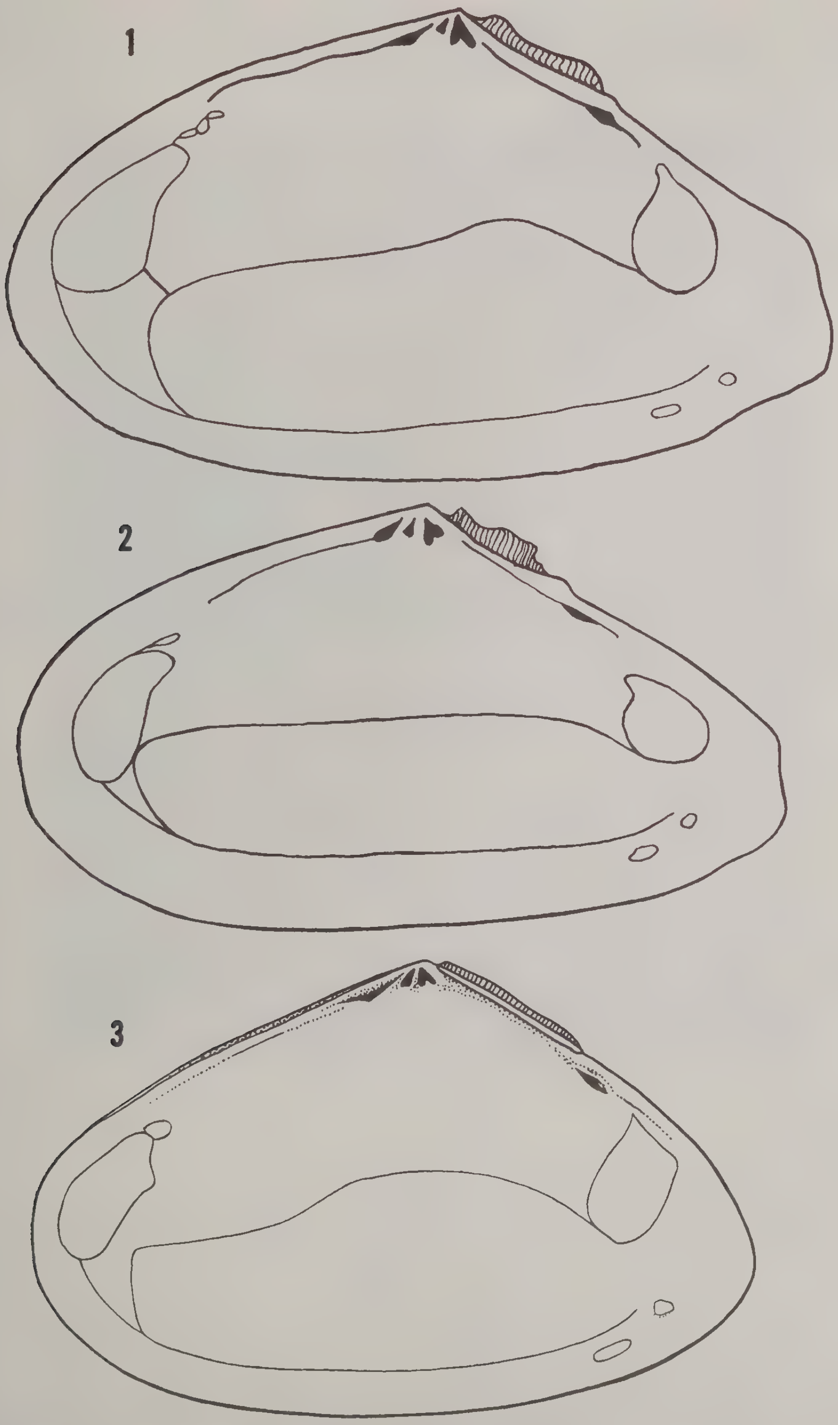

Plate 144. Figs. 1–3. Diagrammatic illustration of the internal surface of the right valve showing the dental configuration and muscle scars. Fig. 1. *Tellina alternata* Say (about 1.9x) [L=65 mm.]. Fig. 2. *Tellina punicea* Born (about 2.9x) [L=40 mm.]. Fig. 3. *Tellina angulosa* Gmelin (about 2.6x) [L=40 mm.].

thickness and the convexity of the shell. Most specimens from the Caribbean, or northernmost extent of the range, tend to possess a thinner shell which is quite compressed while in the southern portion of the range, more specimens have thicker shells which exhibit an increased convexity.

According to Hertlein and Strong (1949) and Olsson (1961) *Tellina punicea* Born is closely allied to *Tellina simulans* Adams of the Eastern Pacific fauna. The former authors who have had the opportunity of comparing a series of both species have concluded that: "The west coast shells are more pointed posteriorly, there is a low depressed area anterior to the posterior angulation on the right valve, and the concentric grooves along the posterior dorsal margin bend more acutely upward than those on the east coast shells." It is also probable that a species, *T. cibaoica*, described by Maury from the Lower Miocene of Santo Domingo represents an early precursor of this complex; it is treated under *Tellina angulosa.*

The species lives in relatively shallow, off-shore waters; it has been taken at 30 feet. Although little information is available as to its substrate preference, many samples have come from soft, black muddy bottoms.

Range. This species appears to be limited to the Caribbean Region and South America. It is found from British Honduras and Jamaica south through the Antilles and along the Caribbean coast of Central and South America and as far south as Estado de Santa Catarina, Brasil.

Specimens examined. British Honduras: Belize (USNM). Nicaragua: Waunta Haulover (USNM; MCZ). Costa Rica: Port Limon (ANSP: USNM). Panama: Bocas de Toro (ANSP); Lobobo Light, Chiriqui Lagoon; mouth of Rio Code del Norte; Fort Sherman, Devil's Beach; Colon (all USNM). Jamaica: Lucea Harbour (USNM); White River Beach (MCZ); Black River; Great Pedro Bay; Kingston; Morant Key (all USNM). Hispaniola. Haiti: Port au Prince; Torbeck; Les Cayes; Saltrou (all USNM). Santo Domingo: Manzanillo Bay (MCZ); Monte Cristi (ANSP; MCZ); Puerto Plata; Santa Barbara de Samana (both MCZ). Puerto Rico: Mayaguez (IMBPR; MCZ); Punta Guanajibo (IMBPR; ANSP; MCZ); Cayos Trios, in 30 feet (IMBPR); Humacao Playa (MCZ); Bahia Bramadero (ANSP). Virgin Islands: St. Thomas (USNM); St. Croix (ANSP). Lesser Antilles: Bridgetown, Barbados (USNM); 2 miles S of Scarborough, Tobago, in 36 fathoms; Trinidad side of the Gulf of Paria; Ortoire River, Mayaro; Manzanilla Beach, Trinidad; Guayaguayare Beach, Trinidad (all MCZ). Colombia: Gulf of Uraba; Punta Brazules (both USNM); Cartagena (USNM; MCZ); Puerto Colombia (USNM). Venezuela: Lake Maracaibo; Beaches at Macuto, Maiquetia (both ANSP); La Guaira; 4.3 kilometers W of Barcelona (both USNM); Guante (ANSP); Cumaná (USNM); Cubagna Island (MCZ); Margarita Island (ANSP). Surinam: Surinam (MCZ). Brasil: Fernando de Noronha; Fortaleza, Ceara; Ilha de Itaparica, Bahia (all MCZ); Ilheus, Bahia (USNM); Vitoria, Espirito Santo (ANSP; MCZ); Carapebus, Espirito Santo; Praia Comprida; Mambucaba, Rio de Janeiro (all MCZ); Rio de Janeiro (ANSP); Ilha de São Sebastiao and Santos, São Paulo (both USNM); Praia Grande, Itanhaém, São Paulo (MCZ); São Francisco do Sul, Santa Catarina (USNM).

Tellina (Eurytellina) trinitatis *Tomlin*

Plate 145, fig. 1–2; Plate 149, fig. 5

Eurytellina trinitatis Tomlin 1929, Jour. Conch., **18**(11): 310 (Colón Harbour, Panamá) [Holotype, BMNH].

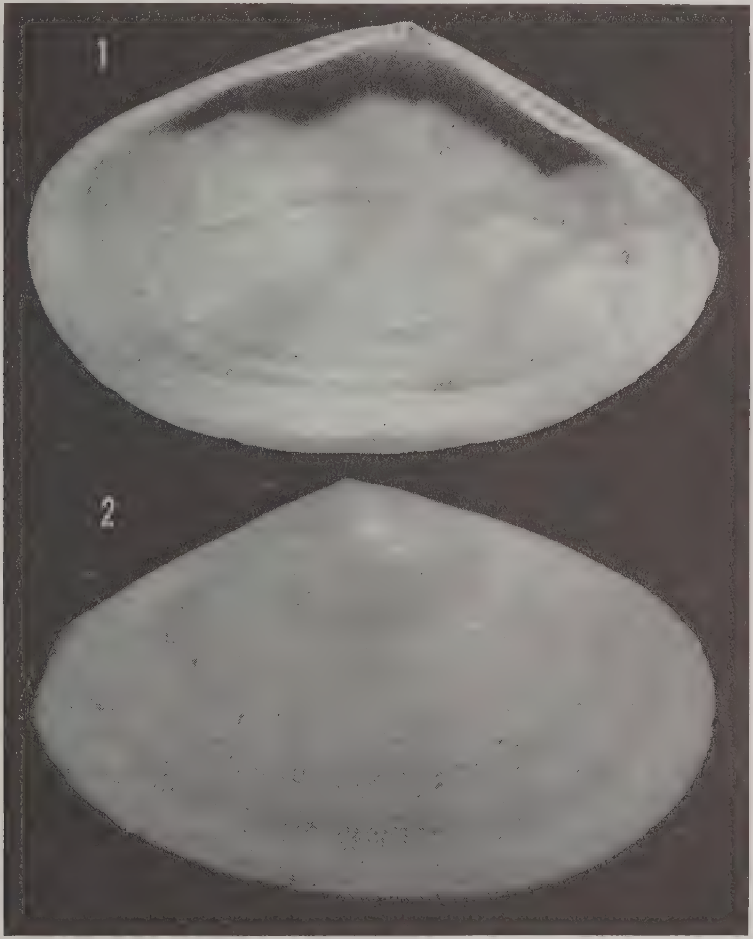

Plate 145. *Tellina trinitatis* Tomlin. Fig. 1. Internal view of the right valve, Payarde, Panamá, MCZ 258317 (about 2.8x) [L=37 mm.]. Fig. 2. External view of the right valve, Marco, Florida, MCZ 258316 (about 4.4x) [L=23 mm.].

Description. Shell extending to 38 mm. (about 1½ inches) in length and to 25 mm. (about 1 inch) in height, elliptical-subtrigonal, equivalve, nearly equilateral, solid, moderately inflated, with both valves of a more or less equal convexity and with an obsolete posterior flexure to the right. Umbos central, but little elevated, not inflated, conspicuous, white in color, smooth and pointed. Anterior margin smoothly and somewhat narrowly rounded; ventral margin convex and rising gently posteriorly; anterior dorsal margin more or less straight, long and gently inclined; posterior dorsal margin straight and long; posterior margin very short and forming an oblique truncation. Sculpture consisting of weak, closely and irregularly spaced concentric bands; sulci poorly incised; weak radial lirations evident. Weak posterior ridge present in both valves. Ligament brown, short, slightly protuberant, set in a lanceolate escutcheon; lunule obsolete. Calcareous portion of the ligament subtended by poorly developed nymphal callosities. Hinge line with strong lateral dentition in the right valve. In the left valve, the cardinal complex consists of an anterior thin bifid tooth with more or less equal lobes and of a thin elongate posterior laminate tooth; no true lateral dentition, but obsolete tubercles present along the hinge line anteriorly and posteriorly. In the right valve, the cardinal complex consists of a posterior, small, slightly thickened bifid tooth with subequal lobes and of an anterior small subdeltoid laminate tooth; anterior lateral tooth well developed, thin, elongate, slightly upcurled and subproximal to the cardinal complex; posterior lateral tooth distal to the cardinal complex, elongate and somewhat upcurled. Internal radial rib obsolete. Adductor muscle scars moderately impressed. Anterior adductor muscle scar irregularly sublunate; posterior adductor scar subquadrate. Pallial sinus hardly rising behind, slightly convex above, extending to, nearly coalescing with, but generally slightly free from the anterior adductor muscle scar, and then falling in a more or less straight short line to the pallial line. The pallial sinus is generally united to the anterior adductor muscle scar by a short straight interlinear scar. Color pink with whitened periphery, posterior slope and umbo; pink coloration more intense internally and often disposed in variable bands externally; in adults a concentrated radial streak of color parallels the posterior ridges externally.

length	height	width	
32.6 mm.	19.4 mm.	7.5 mm.	Holotype of *trinitatis* Tomlin
38.0	25.0	—	off Surinam
36.0	23.5	—	Guantanamo Bay, Oriente, Cuba
25.5	15.5	6.5	Coronie, Surinam
19.5	12.0	5.0	Coronie, Surinam

Remarks. This species is a poorly known member of the *Eurytellina* complex. In the Western Atlantic fauna, it is probably most closely related to *Tellina punicea* Born. *Tellina trinitatis* is not as intensely purple as is *punicea* and the pallial sinus of *trinitatis* is generally separated from the anterior adductor muscle scar. The short oblique posterior margin and the characteristically pointed umbo as well as the convexly rising ventral margin distinguish *trinitatis*. *Tellina angulosa* is also nearly allied but is much different in regard to its sculpture which is stronger and more widely spaced. Further, the right anterior lateral tooth of *trinitatis* is more distally removed from the cardinal complex than it is in either *angulosa* or *punicea*. In the Eastern Pacific, *Tellina prora* Hanley is the analog of *trinitatis*.

Range. This species has been found as far north as Marco, Florida and as far south as Arroyo de Pando, Canelones, Uruguay; however, both of these records may be questioned since the specimens were not complete. Certainly the central concentration of the range of *trinitatis* is the Caribbean Sea; it was taken in abundance in a soft black muddy substrate at 10 fathoms in the Gulf of Venezuela.

Specimens examined. FLORIDA: Marco (MCZ). CUBA: Guantanamo Bay, Oriente (MCZ). PANAMA: Payarde (MCZ, Olsson); Colón (type, BMNH); Fort Sherman, Devil's Beach, 5 miles N of Colón (USNM). VENEZUELA: *Oregon* station 5669, Gulf of Venezuela (MCZ). SURINAM: Coronie Strand (Leiden, Altena). URUGUAY: Arroyo de Pando, Canelones (USNM).

Tellina (Eurytellina) angulosa *Gmelin*

Plate 143, fig. 1; Plate 144, fig. 3; Plate 148, fig. 2

Tellina angulosa Gmelin 1791, Systema Naturae, Ed. 13, p. 3244 (ad insulas Americae) [type locality, here restricted, St. Croix, Virgin Islands; types not seen], *non* Röding 1798, *nec* Renier 1804.

Tellina striata Spengler 1798, Skrivter Naturhistorie Selskabet, Copenhagen, **4**(2): 105 [type locality, here restricted, St. Croix, Virgin Islands; types, Zoological Museum, Copenhagen], *non* Costa 1829.

Tellina laeta Montagu 1804, Testacea Britannica, p. 57 (*pars*).

Tellina punicea 'Born' Lamarck 1818, Animaux s. Vertebres, **5**: 525; d'Orbigny 1853 [in] Sagra, Hist. L'Ile Cuba, Mollusques, **2**: 298 (*pars*).

Donax martinicensis Lamarck 1818, Animaux s. Vertebres, **5**: 552 (Martinique); 1841, Delessert, pl. 6, fig. 15 [types, Museum d'Histoire Naturelle, Paris].

Tellinides rosacea King and Broderip 1832 (*teste* Hanley), Zool. Journ., **5**: 19 (Santos, Brasil) [types not seen].

Tellina hanleyi 'Deshayes MS' H. and A. Adams 1856 (*teste* Dall), Genera Recent Mollusca, **2**: 396, *non* Dunker 1853, *nec* Bertin 1878 (*nomen nudum*).

Tellina subradiata 'Schumacher' Arango 1880, Contrib. Fauna Mala., Cubana, p. 244 (*nomen nudum*).

Tellina (*Eurytellina*) *angulosa* Gmelin. Dall 1900, Proc. U.S. Nat. Mus,, **23**: 294.

Tellina (*Arcopagia*) *angulosa* Gmelin. McLean 1951, New York Acad. Sci., **17**(1): 93.

Tellina (*Eurytellina*) *punicea* 'Born' Gardner 1928, United States Geol. Survey, Prof. Papers 142-e, p. 193, *non* Born 1778.

Description. Shell extending to 50 mm. (about 2 inches) in length and to 38 mm. (about 1½ inches) in height, subtrigonal, nearly equilateral, slightly inflated, with the left valve more convex and with usually a very slight flexure to the right posteriorly. Umbos only slightly posterior to the middle, little elevated, somewhat inconspicuous and often pointed. The anterior margin broadly and smoothly rounded; the ventral margin straight or somewhat convex with a slight postbasal arcuation; anterior dorsal margin gently sloping and short, usually straight, but sometimes convex; posterior dorsal margin rather long and moderately steep; posterior margin short, straight and producing a truncated appearance to the outline of the shell. Sculpture consisting of rather deeply incised concentric sulci separated by rather broad elevated bands; this concentric sculpture is unlike in opposite valves; in the left valve, the elevated bands are broader and the sulci fewer. A slight posterior ridge occurs on the right valve and a concomitant sulcus on the left. Ligament brown, protuberant, set in a narrow escutcheon and subtended by developed nymphal callosities. Hinge line moderately developed. In the left valve, the cardinal complex consists of an anterior, deltoid bifid tooth with subequal lobes and of a posterior, thin laminate tooth which is adpressed to the calcareous element of the ligament; proximally anterior to the bifid cardinal tooth is the small anterior lateral tooth; the distal posterior lateral is moderately well developed. In the right valve, the cardinal complex consists of a posterior, slightly skewed, bifid tooth with subequal lobes and of an anterior thickened laminate cardinal tooth; posterior lateral tooth well developed, strong, and distal; anterior lateral tooth well developed, but weaker than the posterior lateral and located next to the laminate cardinal tooth. A rib extends from the umbonal region to the anterior adductor muscle scar in the left valve. Adductor muscle scars well impressed. Pallial sinus equal in opposite valves, long, rising gently behind, forming a slightly pointed apex far below the umbo, extending almost to but separated and not contiguous with the anterior adductor scar, and falling at a slight angle to the pallial line with which it is extensively confluent. A small interlinear scar often extends between the pallial sinus and the anterior adductor scar. Externally the shell is predominantly white and pink, shining and somewhat glabrous; localized concentrations of pink occur as rays extending from the umbo. There are usually three such radiations, one paralleling the posterior ridge, another in the posterior quarter of the disc and a third along the anterior slope, more or less parallel to the anterior dorsal margin. Tints of yellow or apricot may augment or replace the pink, and rarely specimens may be nearly pure white. Some specimens also have indications of concentric bandings of white and pink. Internally, the shell is polished and usually suffused with white. A peripheral band of white is most often present.

length	height	width	
50.0 mm.	38.0 mm.	—	Altona Lagoon, St. Croix, Virgin Islands
46.0	30.5	12.0	São Paulo, Brasil
40.0	26.0	9.5	Altona Lagoon, St. Croix, Virgin Islands
39.0	26.5	8.0	Boca Chica Key, Florida
37.5	22.5	7.5	Manguinhos, Ilha de Itaparica, Bahia, Brasil

Remarks. Tellina angulosa Gmelin has been variously interpreted by numerous workers; the type figure is in Chemnitz (Conch. Cab., 1st Ed., vol. 10, pl. 120, figs. 1654 and 1655). It may be most easily confused with *Tellina alternata* and some discussion of the important traits which characterize each species have been given (see *Remarks* under *T. alternata*). *Tellina angulosa* is typically subtrigonal, its height is higher in proportion to its length when compared with *T. alternata.* In addition, the orange-red rays which color the umbonal region of *angulosa* are distinctive. In the northernmost extension of its range, *angulosa* overlaps with the range of *alternata.* In certain areas of Florida, *angulosa* tends to possess a thicker and heavier shell; the shell may exhibit more elongate proportions, but usually the posterior dorsal slope maintains a typical convexity which is diagnostic. Since some lots from southern Florida are mixed or nearly impossible to distinguish, it is possible that hybridization is occurring; however, some different or peculiar ecological conditions may prevail in certain areas to which *angulosa* has become adapted.

Tellina punicea Born, which is almost completely Caribbean in its distribution, may also be confused with *T. angulosa*, but in the latter, the pallial sinus remains distinctly free from the anterior adductor muscle scar and the orange-red coloration of the shell never approaches the intense purple-red of *T. punicea.*

The fossil history of *Tellina angulosa* has its recognizable beginning in the Miocene. *Tellina roburina* Dall from the Oak Grove Sands in Florida is markedly similar to *angulosa.* Gardner (1928) records the presence of *T. roburina* in the Alum Bluff formation of the Middle Miocene; she mentions that the lateral teeth attain a greater strength and are somewhat farther removed from the cardinal complex than similar modern forms. Maury (1917) described *Tellina cibaoica* from the Lower Miocene of Santo Domingo which though comparable to the recent *Tellina punicea* Born, is by virtue of its subtrigonal shape quite similar to *angulosa.* In the Bowden formation of Jamaica, none of the *Eurytellina* bears a resemblance to *angulosa.*

Although *Tellina rubescens* Hanley of the Eastern Pacific has been considered an analog of *T. angulosa*, it is certainly quite dissimilar in regard to the pallial sinus which is coextensive with the anterior adductor muscle scar. *Tellina eburnea* Hanley (=*panamensis* Li; =*liliana* Hertlein and Strong) is comparable in shape, in outline, and in the configuration of the pallial sinus; it differs from *angulosa* in its heavier valves and pure white coloration.

Range. This species is found as far north as the southeastern and southwestern coasts of Florida. It occurs along the Gulf and Caribbean coasts of the Yucatan Peninsula and throughout the Greater and Lesser Antilles south to Brasil and Uruguay.

Specimens examined. FLORIDA: Virginia Key (MCZ); Biscayne Bay (Bulloch; ANSP); Boca Chica Key (MCZ); East Cape Sable; Marco Beach and Marco River (all D. and N. Schmidt); Sarasota Bay (USNM). MEXICO: Isla del Carmen (MCZ). Campeche; Yucatan (both ANSP). BRITISH HONDURAS: Belize (USNM). GUATEMALA: Puerto Barrios (ANSP). PANAMA: Payarde (Olsson). CUBA: *Barrera* station 220, Havana; *Barrera* station 213, Varadero Beach; *Barrera* station 221, Cardenas, in 1–3 fathoms (all USNM); Icacos Peninsula, in 3–4 fathoms (ANSP). JAMAICA: Green Island Harbour, Hanover; Black River, St. Elizabeth (both USNM); Little Goat Island, Portland Bight (MCZ). HISPANIOLA. HAITI: Bizoton; Aquin (both USNM). SANTO DOMINGO: Monte Cristi (MCZ); Puerto Plata (USNM); Santa Barbara de Samana (USNM; MCZ). PUERTO RICO: Punta Guanajibo (ANSP; MCZ); Ponce; La Parquera (both MCZ); Las Croahas, Fajardo (ANSP). VIRGIN ISLANDS: Magen's Bay, St. Thomas (ANSP); St. John's (ANSP; MCZ); Altona Lagoon, St. Croix (MCZ). LESSER ANTILLES: Guadeloupe (ANSP; MCZ); Roseau, Dominica (ANSP); St. Lucia, in 10 fathoms (USNM; MCZ); Chaguaramas Bay, Trinidad (USNM); Guayaguayare Beach, Trinidad (MCZ). VENEZUELA: Cumana (USNM); Margarita Island (MCZ). BRASIL: Praia Grande and Manguinhos, Ilha de Itaparica, Bahia; Pedra Furada, Bahia (all MCZ); Ilha Grande, Federal District (USNM); Praia de Caraquatatuba, São Paulo; São Paulo (both MCZ). URUGUAY: Arroyo de Pando, Canelones (MCZ).

Tellina (Eurytellina) alternata *Say*

Plate 144, fig. 1; Plate 146, figs. 2–4

Tellina alternata Say 1822, Jour. Acad. Nat. Sci., Philadelphia, **2:** 275; 1833 (?) Conrad [*in*] Say, American Conchology, **7:** pl. 65, fig. 1 (inhabits the coast of Georgia and East Florida) [type locality, here restricted, Sea Island, Georgia; holotype apparently lost].

Tellina (Peronaeoderma) alternata Say. H. and A. Adams 1856, Genera Recent Mollusca, **2:** 396.

Tellina planulata Sowerby 1867 [*in*] Reeve, Conch. Icon., **17, Tellina,** pl. 33, fig. 186 (type locality unknown) [type locality, here restricted, Sea Island, Georgia; holotype, BMNH, no. 74.12.11.244].

Tellina (Eurytellina) alternata Say. Dall 1900, Trans. Wagner Free Inst. Sci., Philadelphia, **3**(5): 1029.

Description. Shell extending to 72 mm. (about $2\frac{3}{4}$ inches) in length and to 40 mm. (about $1\frac{1}{2}$ inches) in height, elongate-subtrigonal, slightly inequilateral, somewhat compressed with the left valve slightly more convex and with a gentle flexure to the right posteriorly. Umbos slightly posterior to the middle, scarcely elevated, small, and often pointed. Anterior margin smoothly and broadly rounded; ventral margin more or less straight and rising posteriorly in a gentle arcuation; anterior dorsal margin gently sloping, convex and rather long; posterior dorsal margin straight, not too steeply sloping and very long; posterior margin extremely short, straight, rarely perpendicular to the dorsoventral axis. In outline, the shell appears to be attenuate posteriorly with a slight but marked truncation. Sculpture consisting of incised concentric sulci separated by broad bands. A discrepancy exists between the valves; the left valve has broader bands and less sulci. A posterior ridge occurs in the right valve and a poorly developed concomitant sulcus on the left valve. Ligament light brown to black, strong, protuberant, and set in an ill defined escutcheon. Calcareous portion of the ligament well developed and subtended by nymphal callosities. Hinge line moderately developed. In the left valve, the cardinal complex consists of an anterior somewhat strong, bifid cardinal tooth with equal lobes and of a posterior, thin, laminate tooth which is often broken or lost. Proximally anterior to the bifid cardinal tooth is a rather well developed, but small lateral tooth; the distal posterior lateral tooth is weakly developed or obsolete. In the right valve, the cardinal complex consists of a posterior skewed, moderately strong bifid tooth with the posterior lobe the larger and of an anterior, thickened laminate cardinal tooth; anterior lateral tooth small, thin, and located next to the laminate cardinal tooth; posterior lateral tooth distal and stronger. In both valves an internal rib extends from the umbo to the anterior adductor muscle scar. Adductor muscle scars usually well impressed. Pallial sinus equal in both valves, rising slightly to a high point far beneath the umbos and extending far anteriorly near to but not contiguous with the anterior adductor scar. Often a small linear scar connects the pallial sinus with the anterior adductor scar. The pallial sinus falls arcuately to the pallial line; confluence extensive. Externally, the shell is shining, glabrous, and nearly always white, often with slight suffusions of pink or yellow; a yellowish-brown periostracum may augment the superficial coloration. Internally, the base color is a polished white with suffusions of yellow and rarely pink or apricot.

length	height	width	
68.0 mm.	37.8 mm.	12.0 mm.	Holotype of *planulata* Sowerby
72.0	40.0	13.0	Amelia Island, Florida
55.0	29.5	9.5	Cocoa Beach, Florida
50.5	32.0	13.5	Biscayne Bay, Florida
49.0	28.0	11.0	Fort Myers Beach, Florida
44.5	25.5	9.5	Treasure Island, off Pasadena, Florida

Remarks. Tellina alternata is one of the largest and most common tellens of the Atlantic coast of North America. It appears to prefer the sandy substrates along the shelf region in depths from 10–70 fathoms. It is typically elongate, white and with some yellowish suffusions internally. Its similarity to a number of other species is remarkable. With *Tellina nitida* Lamarck of European waters, it may be confused because of the similarity in shape and coloration, but the lack of eurytellinid dentition in *nitida* as well as the absence of intercalated sculpture on the posterior slope of *alternata* serve sufficiently to distinguish each species. Records of *alternata* in European waters have, no doubt, been established upon its outward similarity to *nitida*.

Certain species in the Western Atlantic with which *alternata* may be confused include *T. tayloriana* and *T. angulosa. Tellina tayloriana* has been considered a synonym of *alternata* by some authors (Dall 1900a) but herein both species are recognized in accordance with the interpretation of Olsson and Harbison (1953). Traits which distinguish *tayloriana* and *alternata* are discussed elsewhere (see *Remarks* under *T. tayloriana*). Color is the simplest and, in this case, one of the most reliable characteristics employed to distinguish *tayloriana*, which is pink, and *alternata*, which is white or yellow-white. There appears to be a slight overlapping in the ranges of these species along the Gulf coast and no clear cut line separates the populations.

Tellina angulosa Gmelin replaces *T. alternata* in the Antillean and Caribbean Regions. In general, *alternata* is much more elongate than *angulosa* and, therefore, less subtrigonal. The sculptural pattern of *alternata* is dissimilar in opposite valves. The right valve has the concentric sculpture more crowded with the concentric band consequently narrowed; the left valve possesses proportionally fewer sulci and consequently the sculpture is less crowded with the concentric bands broader. The right valve has from four to nine more sulci per centimeter than the left. In contradistinction to this condition, *T. angulosa* possesses valves upon which the concentric sculpture is less dissimilar. This characteristic is best employed in conjunction with a discreet appraisal of shape and color. *Tellina angulosa* has a tendency to have an anterior and a posterior orange-red ray emanating from the umbonal region; the shell tends to be thinner and more translucent; the angle of declination of the posterior dorsal slope is steeper and the margin itself is more convex than *alternata*.

In the Eastern Pacific, the subgenus *Eurytellina* is considerably richer in species but no single species from this region may be recognized as an analog of *Tellina alternata*. In general outline, *T. laceridens* Hanley and *T. hertleini* Olsson approach *alternata* but the pallial sinus is confluent with the anterior adductor muscle scar in both of the former.

In the fossil record, *Tellina alternata* has been recorded in the Pleistocene of the Gulf States by Maury (1920), the Pliocene of Florida by Dall (1900b), Olsson and Harbison (1953), and in the Pliocene of the Carolinas by Tuomey aud Holmes (1857). Mansfield (1932) has given also a record from the upper Miocene of Harver's Creek, Florida. From the Lower Miocene of Santo Domingo, Maury (1917) has described *Tellina riocanensis* which bears some resemblance to *alternata* and is a probable ancestor to the recent species.

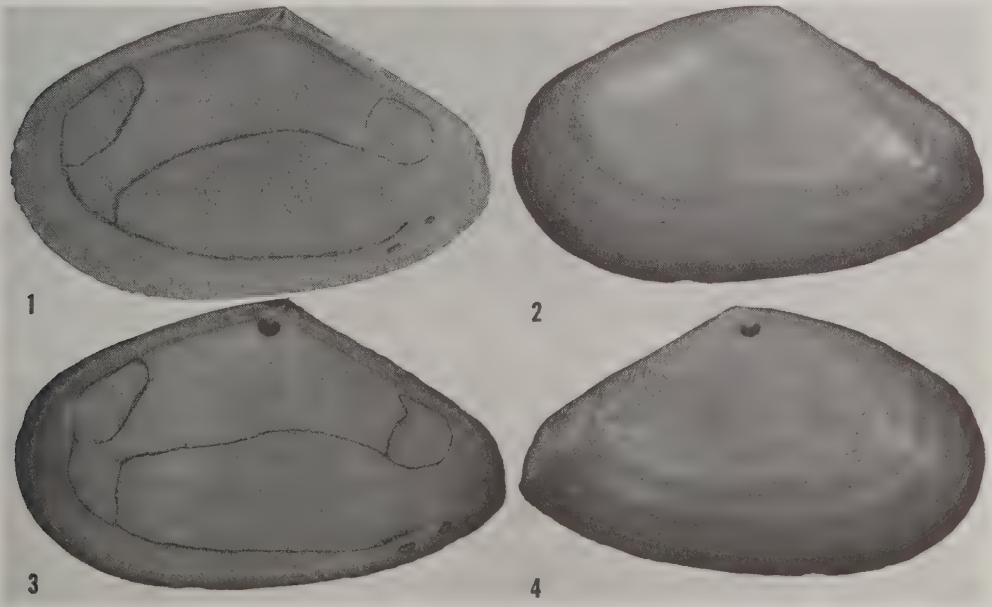

Plate 146. Fig. 1. *Tellina tayloriana* Sowerby, internal view of the right valve of the holotype, Mexico, BMNH (about 1.2x) [L=57.8 mm.]. Figs. 2–4. *Tellina planulata* Sowerby [=*Tellina alternata* Say]. Fig. 2. External view of the left valve of the holotype. Fig. 3. Internal view of the right valve of the holotype. Fig. 4. External view of the right valve of the holotype, no locality given, BMNH (about 1x) [L=68 mm.].

Range. This species occurs along the Atlantic and Gulf coasts of the United States from Cape Hatteras, North Carolina south through the Florida Keys around the Gulf of Mexico to Matagorda Island, Texas. Records and ranges published by Dall (1889) and others mention the occurrence of this species in the Antillean and Caribbean areas. This is not probable, for specimens from Haiti, Santo Domingo, British Honduras, and Puerto Rico which have been examined appear to be referable to *Tellina angulosa* Gmelin.

Specimens examined. North Carolina: Cape Hatteras: *Albatross I* station 2275, 19 miles NE of Cape Hatteras (35°20′ N; 75°18′ W), in 16 fathoms; *Albatross I* station 2112, 15 miles NNE of Cape Hatteras (35°20′ N; 75°13′ W), in 15½ fathoms; *Albatross I* station 2596, 19 miles SE of Cape Hatteras (35°05′ N; 75°10′ W), in 49 fathoms; *Albatross I* station 2609, 20 miles SEE of Cape Lookout (34°26′ N; 76°12′ W), in 22 fathoms; Fort Macon, Beaufort (all USNM); Bird Shoal, Beaufort; Shark Shoal, Boque Sound (both ANSP); Boque Id.; Shackleford Id. (both MCZ); Middle Sound, near Wilmington (USNM); Cape Fear, Smith Id. (ANSP). South Carolina: Merry's Inlet (MCZ); Cain Hoy, Wando (post Pliocene, USNM); Isle of Palms (CM; ANSP; MCZ); Charleston (CM; USNM; MCZ); Edisto Beach (CM). Georgia: Sea Id. (ANSP; MCZ); St. Simon's Bay (USNM). Florida: Fernandino Beach (D. and N. Schmidt; USNM); Amelia Id. (ANSP; USNM); Mayport (ANSP); Jacksonville Beach (ANSP; MCZ); mouth of St. Johns River; St. Augustine (both ANSP); beach N of St. Augustine Inlet (MCZ); Matanzas Inlet (ANSP); 4 miles NE of Daytona Beach, in 10 fathoms (USNM); Coronado Beach; Cape Canaveral; Cocoa Beach; 2 miles SE of Cocoa Beach, in Banana River; Atlantic Beach (all MCZ); Fort Pierce, Hutchinson Id. (D. and N. Schmidt); North Inlet, Lake Worth (ANSP); off Lantana, in 70 fathoms; Fair Isle Basin, Biscayne Bay; Virginia Key (all MCZ); Hawk Channel, in 3–4 fathoms (USNM); 4 miles NNE of The Elbow, Key Largo, in 66 fathoms (MCZ); Lower Matecumbe Key; 3 miles SSE of Key West (both USNM); Boca Grande Key; NW of Dry Tortugas, in 10 fathoms (both MCZ); Madeira Bay, Florida Bay (CNM); Marco; Bonita Springs; Fort Myers Beach; Blind Pass, Sanibel Id. (all D. and N. Schmidt); 2 miles and 30 miles W of Sanibel Id. (both MCZ); Boca Grande, Little Gasparilla; Punta Gorda Beach (both ANSP); Charlotte Harbor; Long Boat Key; Anna Maria Key; Mullet Key (all USNM); Tampa Bay (ANSP; USNM); Treasure Id.; Boca Ceiga Bay (both MCZ); Pass-a-grille (USNM; MCZ); Clearwater (MCZ); Cedar Key (USNM; MCZ); Alligator Harbor (ANSP; MCZ); Indian Pass, Apalachicola Bay (ANSP); Port St. Joe (MCZ); Beacon Beach (ANSP); Panama City (USNM); Pensacola (MCZ). Mississippi: Horn Id. (ANSP). Louisiana: Chandeleur Id.; Grand Isle; Cameron; Grand Lake (all USNM). Texas: High Id., Bolivar Peninsula (MCZ); Galveston (ANSP; USNM; MCZ); Padre Id., Corpus Christi (USNM); Sebrile Banks, off Padre Id. (ANSP); Matagorda Id. (MCZ).

Tellina (Eurytellina) tayloriana *Sowerby*

Plate 146, fig. 1

Tellina tayloriana Sowerby 1867 [*in*] Reeve, Conch. Icon., **17, Tellina,** pl. 30, fig. 168 (Mexico) [type locality, here restricted, Tampico, Mexico; holotype, BMNH, no. 74.12.11.318].

Tellina taylori Sowerby 1867, American Jour. Conch., **3:** 327, error for *tayloriana*.

Tellina (Eurytellina) tayloriana Sowerby. Olsson and Harbison 1953, Pliocene Mollusca of Southern Florida, Acad. Nat. Sci., Philadelphia, Monograph 8, p. 124, pl. 14, figs. 1–1b.

Description. Shell extending to 60 mm. (about 2½ inches) in length and to 36 mm. (about 1½ inches) in height, elongate subtrigonal, slightly inequilateral, slightly compressed with the right valve somewhat flattened, and with a weak flexure to the right posteriorly. Umbos only slightly behind the middle, little elevated, rather small and inconspicuous, and often sharply pointed. Anterior margin broadly and smoothly rounded; ventral margin usually slightly convex with a gently rising postbasal arcuation; anterior dorsal margin rather long, gently sloping and straight; posterior dorsal margin long, straight, and not steeply sloping; posterior margin short, straight, and at an angle to the dorso-ventral axis. In outline, the shell appears somewhat attenuate and truncate posteriorly. Sculpture consisting of incised concentric sulci, separated by broad bands. A discrepancy exists between the valves, the sulci are more dense on the right valve with concomitantly narrower bands. Ligament brown, protuberant and set in a narrow ill-defined escutcheon. The posterior dorsal slope of the left valve is flattened and broad. Calcareous portion of the ligament subtended by moderately developed nymphal callosities in both valves. Hinge line moderately developed. In the left valve, the cardinal complex consists of an anterior deltoid bifid tooth with subequal lobes and a posterior thin weak laminate cardinal tooth partly adpressed to the calcareous portion of the ligament and often broken or lost in some specimens; proximally anterior to the cardinal complex is a variously developed lateral tooth; the distal posterior lateral tooth is weak or obsolete. In the right valve, the cardinal complex consists of a posterior skewed, strong, deltoid bifid tooth with the posterior lobe the larger and of an anterior thin, elongate laminate cardinal tooth; anterior lateral tooth small and thin and very close to the laminate cardinal; posterior lateral rather well developed and distal to the cardinal complex. A heavy and well developed rib extends from the umbonal region to the anterior adductor scar in both valves. Adductor muscle scars well impressed. Pallial sinus rather variable, but usually subequal in each valve, flattened above, extending anteriorly but usually not contiguous with the anterior adductor. Sometimes an interlinear scar may connect the anterior adductor and the pallial sinus. The sinus falls rather abruptly and straight to the pallial line; confluence entire. Externally, the shell is white suffused with pink, with some alternations in bands of color, and with a darkening of the pink to nearly brownish peripherally. Internally, the shell is predominantly pink with some white suffusion and bands.

length	height	width	
57.8 mm.	34.5 mm.	11.7 mm.	Holotype of *tayloriana* Sowerby
60.0	36.0	11.5	Tampico, Mexico
54.5	30.5	11.5	Mustang Id., Texas
52.0	30.5	9.5	Corpus Christi, Texas
37.0	22.5	7.0	Port Isabel, Texas

Remarks. Heretofore, most authors, including Dall, have considered *Tellina tayloriana* Sowerby as a synonym of *Tellina alternata* Say. Recently Olsson and Harbison (1953) have differentiated these two species and have documented their occurrence in the Pliocene at Clewiston, Florida; they have gone so far as to infer that many fossil records of *T. alternata* are in reality those of *T. tayloriana.* Parker (1960) in his ecological studies of the macroinvertebrate fauna of certain areas along the Gulf of Mexico has recognized the existence of *T. tayloriana* which he included as an important element in the inner shelf fauna (2–12 fathoms) along the coast of Texas.

In the Recent fauna, *Tellina tayloriana* appears to possess a discontinuous distribution; however, the records of the occurrence of this species along the Atlantic coast of Florida near St. Augustine and the area around Charleston, South Carolina are of doubtful authenticity. Notwithstanding these reservations, the central populations of *tayloriana* are to be found west of the Mississippi River.

There is no doubt that *tayloriana* and *alternata* are extremely closely related, but enough characteristics appear to distinguish each so that the treatment accorded these species by Olsson and Harbison seems justified. In color, *tayloriana* is bright pink, and this coloration appears to be present through the whole shell and is not disposed in distinct rays or patterns. The interior of the valves are generally highly polished with strong muscle impressions and a well differentiated and broad anterior radial rib. In contrast to *T. alternata*, the internal cavity of *tayloriana* is narrower, a trait reflected by the shallowness of the concavity of both valves. The right valve of *tayloriana* is noticeably more flat than that of *alternata*. The anterior dorsal marginal plate, present in each valve and adpressed when the valves are closed, is broad and flattened; in the right valve this structure carries the anterior lateral tooth. Externally, the anterior dorsal surface of the left valve possesses in a well developed state the concentric sculptural pattern; in *alternata*, the concentric sulci in this region are less well defined, poorly developed and more widely separated by concentric bands. It appears that *tayloriana* and *alternata* may be ecologically separated; there is some evidence which indicates that *tayloriana* lives in off-shore waters at greater depths than *alternata*.

Range. This species appears to be localized along the Gulf Coast of Texas and Mexico; the records from South Carolina and Florida are subject to questionable authenticity.

Specimens examined. SOUTH CAROLINA: Charleston (MCZ). FLORIDA: St. Augustine (USNM; MCZ). TEXAS: High Id., Bolivar Peninsula (ANSP); Galveston (ANSP; MCZ); Matagorda Id. (USNM; MCZ); Port Aransas (ANSP; MCZ); Mustang Id.; Corpus Christi (both MCZ); Freeport (Bulloch); Port Isabel; Boca Chica Beach, 3 miles N of Rio Grande (both MCZ); Brazas Id. (ANSP); Rio Grande (USNM). MEXICO: Tampico; Tuxpan; 15 miles N of Tecolutla (all MCZ).

Tellina (Eurytellina) nitens *C. B. Adams*

Plate 147, figs. 3–4; Plate 148, fig. 1; Plate 149, fig. 4; Plate 150, fig. 1

Tellina nitens Adams 1845, Proc. Boston Soc. Nat. Hist., **2:** 10 (Jamaica), *non* Deshayes 1854, *nec* Gregorio 1890, *nec* 'Lea' Dall 1900; Clench and Turner, 1950, Occ. Papers. Moll., Harvard University, **1**(15); 317, pl. 44, figs. 3-4 [holotype, MCZ 155606].

Tellina (*Angulus*) *nitens* Adams. Tryon 1869, American Jour. Conch., **4:** 94.

Tellina nitida Lamarck var. *Carolinensis* Dall 1889, Bull. U.S. Nat. Mus., **37:** 60, *non* Conrad 1875 (*nomen nudum*).

Tellina (*Eurytellina*) *georgiana* Dall 1900, Proc. U.S. Nat. Mus., **23:** 294, 310, pl. 2, fig. 3 (*Albatross I* station 2387, 66 miles S of Mobile Bay, Gulf of Mexico (29°34′ N; 88°04′ W), in 32 fathoms) [holotype, USNM 93777], *non* Gabb 1876.

Tellina (*Eurytellina*) *inaequistriata* 'Donovan' Dautzenberg 1900, Mem. Soc. Zool., Paris, **13:** 260, *non* Donovan 1802.

Description. Shell extending to 39 mm. (about 1½ inches) in length and to 21 mm. (about ¾ inch) in height, elongate-elliptical, slightly inequilateral, moderately compressed with the left valve markedly more convex than the right and equivalve with a very slight posterior flexure to the right. Umbos just posterior to the middle, somewhat inflated, slightly raised above the hinge line and somewhat pointed. Anterior margin smoothly and narrowly rounded; ventral margin straight, rising gently posteriorly; anterior dorsal margin long, gently sloping and slightly convex; posterior dorsal margin variable in length, straight and gently sloping; posterior margin straight and at an angle to the dorso-ventral axis. In outline, the posterior portion of the shell appears attenuate, truncate and slightly alate above. Sculpture consisting of finely incised concentric sulci separated by narrow bands; various irregularities occur over the disc where some sulci tend to assume a pattern out of phase with the concentric growth lines. The posterior portion of the right valve is characterized by stronger, less dense concentric bands or riblets. Posterior ridge well developed in the right valve and with a concomitant sulcus in the left; the peculiar posterior riblet sculpture begins either just anterior to or upon the posterior ridge. Ligament light brown, strong, somewhat sunken in a narrow deep escutcheon. Calcareous portion of the ligament subtended by poorly developed nymphal callosities. Hinge line moderately developed. In the left valve, the cardinal complex consists of an anterior, narrow, weak, bifid tooth with subequal lobes and a posterior thin laminate tooth adpressed to the calcareous portion of the ligament and often broken or lost; subproximal anterior lateral tooth weak or obsolete; distal posterior lateral tooth rather poorly developed and weak but stronger than the anterior lateral. In the right

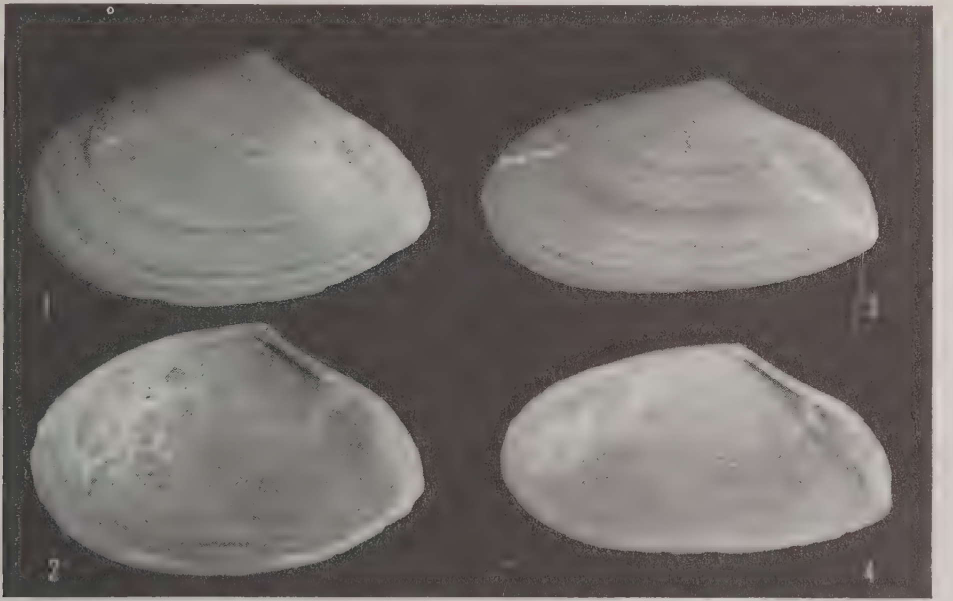

Plate 147. Figs. 1–2. *Tellina decussatula* C. B. Adams [= *Tellina lineata* Turton]. Fig. 1. External view of the left valve of the lectotype. Fig. 2. Internal view of the right valve of the lectotype, Jamaica, MCZ 156459 (about 2.4x) [L = 25 mm.]. Figs. 3–4. *Tellina nitens* C. B. Adams. Fig. 3. External view of the left valve of the holotype. Fig. 4. Internal view of the right valve of the holotype, Jamaica, MCZ 155606 (about 3x) [L = 18.5 mm.].

valve, the cardinal complex consists of a posterior, strongly skewed, usually strong, bifid tooth with the posterior lobe the larger, and an anterior thickened, subdeltoid, strong laminate cardinal tooth; the anterior lateral tooth is subproximal to the laminate of the cardinal complex, strong and well developed; the posterior lateral tooth is distal, moderately well developed and slightly weaker than the anterior lateral. A radial rib extends from the umbonal region to the anterior adductor scar and it is stronger in the left valve. Adductor muscle scars fairly well impressed. Pallial sinus convex above with a slight apex in front of the posterior adductor, extending nearly to the anterior adductor scar but most often not touching it. The pallial sinus descends in an arcuation to the pallial line; confluence entire. Externally, the shell is pink or apricot in color with some interspersed bands of white; the posterior slope tends to be whitish; internally, a pink or apricot color suffused with white occurs; the periphery is white.

length	height	width	
18.5 mm.	10.5 mm.	4.0 mm.	Holotype of *nitens* Adams
32.2	17.2	7.1	Holotype of *georgiana* Dall
39.1	21.3	8.2	Montego Bay, Jamaica
28.0	15.2	6.5	Lucea Bay, Jamaica
24.5	14.0	5.5	off Port Isabel, Texas
11.2	6.2	2.2	*Albatross I* station 2610, 34°20′ N: 76°12′ W, 27 miles SE of Cape Lookout, North Carolina

Remarks. *Tellina nitens* is distinguished from all its near relatives in the subgenus *Eurytellina* by a peculiar vitreous, apricot-colored external surface and an intercalated concentric sculpture along the posterior slope of the right valve. Dall originally related

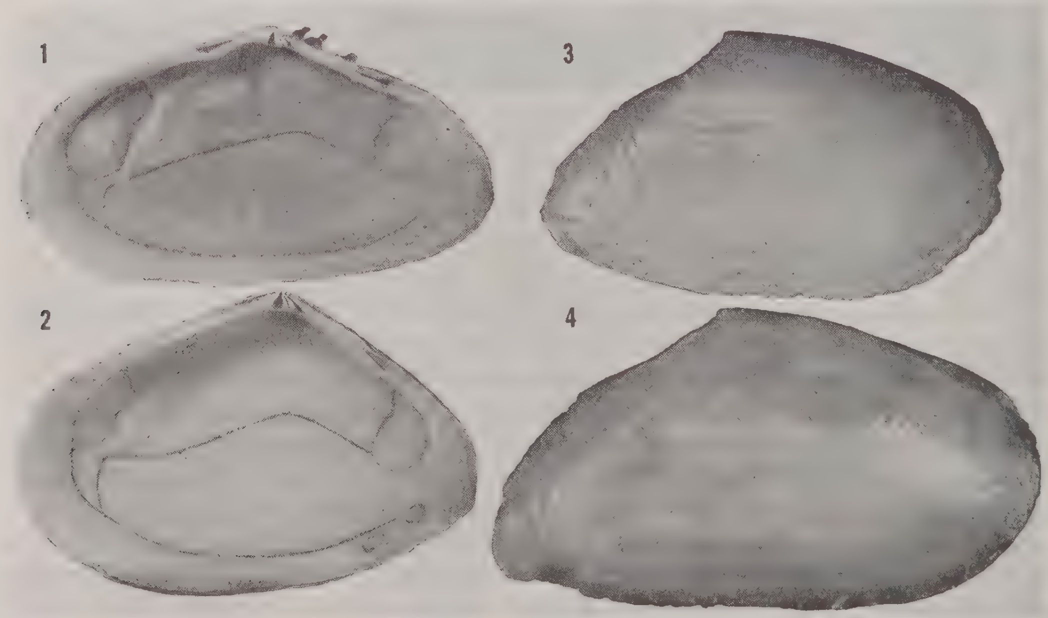

Plate 148. Fig. 1. *Tellina nitens* C. B. Adams, internal view of the right valve, Lucea Bay, Jamaica, MCZ 212137 (about 2.6x) [L=26 mm.]. Fig. 2. *Tellina angulosa* Gmelin, internal view of the right valve, St. Croix, Virgin Islands, MCZ 236382 (about 1.4x) [L=48 mm.]. Figs. 3–4. *Tellina vespuciana* d'Orbigny. Fig. 3. External view of the right valve, Livingston, Guatemala, MCZ 239109 (about 11x) [L=6 mm.]. Fig. 4. External view of the right valve of a syntype, Jamaica, BMNH (about 12x) [L=6.5 mm.].

this species to *Tellina nitida* Lamarck of European seas and called it a variety, *carolinensis.* Later, he recognized its distinctiveness and placed it within *Eurytellina* as *T. georgiana*, a name preoccupied by Gabb. Superficially, *T. nitida* may be confused with *T. nitens*, but the former lacks the eurytellinid syndrome, particularly the developed lateral teeth in the right valve. With some specimens of *T. alternata*, *nitens* may be confounded, but the former lacks a differentiated posterior slope sculpture in the right valve. In point of fact, the anterior right lateral tooth of *T. nitens* is farther removed from the cardinal complex than it is in *alternata*, *punicea* or *angulosa*, and in respect to this character, *nitens* most closely approaches *T. guildingii.* However, *T. guildingii* may readily be distinguished from *nitens* by its closely set, finely incised, concentric sulci and its radial color pattern. To *T. vespuciana*, the smallest and apparently one of the rarest *Eurytellina* of the Western Atlantic, *nitens* is also closely allied by the differential sculpture on the posterior slope of the right valve, but in *vespuciana* this sculpture tends only to be stronger and not intercalated as it is in *nitens* and the strength of the posterior ridge and posterior flexure to the right, in *vespuciana*, are adequately distinctive traits.

Among some of the variations apparent in *Tellina nitens*, none is so obvious as the difference in coloration. Some individuals are apricot or peach in color with brilliantly lustrous surfaces whereas others tend toward pink suffusions and still fewer tend to be

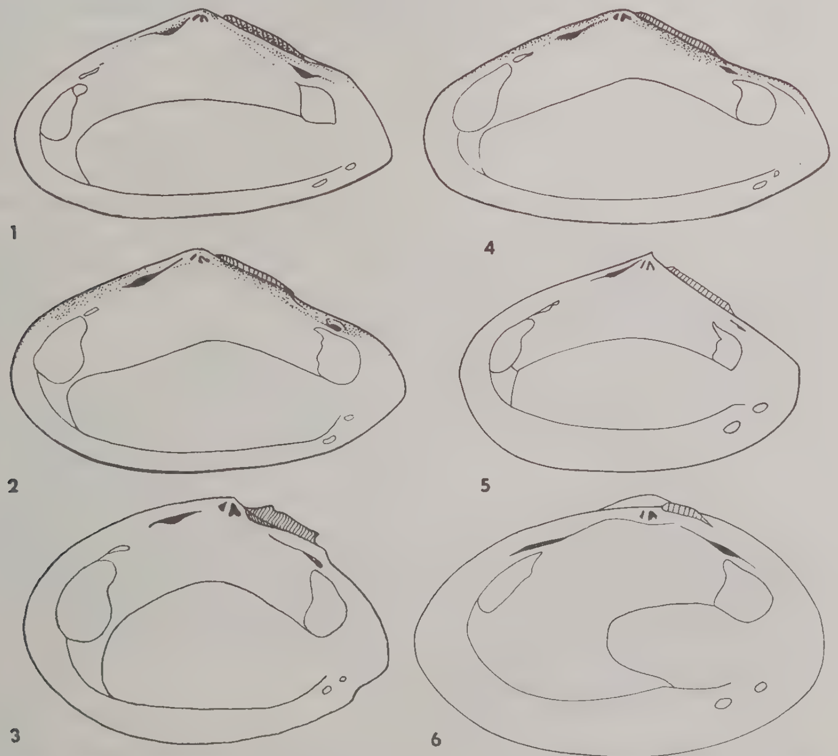

Plate 149. Figs. 1–6. Diagrammatic illustration of the internal surface of the right valve showing the dental configuration and muscle scars. Fig. 1. *Tellina vespuciana* d'Orbigny (about 9x) [L=6 mm.]. Fig. 2. *Tellina guildingii* Hanley (about 2x) [L=30 mm.]. Fig. 3. *Tellina lineata* Turton (about 1.9x) [L=30 mm.]. Fig. 4. *Tellina nitens* Adams (about 2x) [L=30 mm.]. Fig. 5. *Tellina trinitatis* Tomlin (about 1.5x) [L=32 mm.]. Fig. 6. *Tellina americana* Dall (about 9x) [L=7 mm.].

more predominantly white. The placement of the pallial sinus is not always constant; in some specimens, the pallial sinus appears to be coalescent with the anterior adductor muscle scar whereas in others it falls just short of connecting to the scar: even opposite valves may be unlike in this regard. The umbos are particularly pointed, protuberant and conspicuous in the young of *nitens*, and the prodissoconch is smooth, shining and often devoid of any indication of sculpture.

In the Eastern Pacific, *Tellina inaequistriata* Donovan represents the nearest ally to *T. nitens.* They are no doubt analogous and have arisen from a common stock. Records from the Western Atlantic which have cited the occurrence of *T. inaequistriata* represent *T. nitens.* The species are similar in proportion and in coloration but they may be separated by the differentiated posterior slope sculpture which in *inaequistriata* is more extensive, being found on the posterior portion of the disc and the concentric sculpture itself appears to be finer. According to Olsson (1961), *T. inaequistriata* is unique in the possession of fine crenulations along the anterior ventral margin of the shell.

The fossil history of *Tellina nitens* may be traced back to the Lower Miocene, and fossil species which apparently are antecedents of *nitens* have been found in numerous Tertiary deposits in the Caribbean area. Olsson and Harbison (1953) have described *Tellina strictolineata* from the Pliocene of southern Florida, and Woodring (1925) has figured, from the Miocene Bowden marls of Jamaica, *Tellina browni* which has an outline as well as the protuberant umbos similar to *Tellina nitens. Tellina hallistrepta* Dall (1900b) from the Bowden formation appears to be more closely allied to *Tellina* (*Phyllodina*) *persica.* In all these cases, the resemblance of the fossil to the living species is obvious and each species might be assumed to be a precursor to the Recent form. It is of interest to note that there appears to be a trend in the phylogeny of *Tellina nitens.* The characteristic intercalated sculpture of the posterior slope seems to have progressed posteriorly, for in the Miocene species and even in the Pliocene species, the extent of the peculiar sculpture is greater. In the fossil species, this sculpture occurs on part of the disc as well as on the posterior slope and through time the extent of this sculpture has been gradually diminished, so that in *nitens*, it is more or less limited to the bounds of the posterior slope.

Range. This species is found as far north as Cape Hatteras, North Carolina and as far south as Tobago in the Lesser Antilles; it occurs in the Gulf of Mexico along the southwestern coast of Texas and the western tip of Pinar del Rio, Cuba.

Specimens examined. NORTH CAROLINA: *Albatross I* station 2276, 17 miles NNE of Cape Hatteras (35°20′ N; 75°19′ W), in 16 fathoms; *Albatross I* station 2596, 19 miles SE of Cape Hatteras (35°08′ N; 75°10′ W), in 49 fathoms; *Pelican* station 190-1, 9 miles SW of Cape Hatteras (35°06′ N; 75°32′ W), in 11 fathoms; *Albatross I* station 2610, 27 miles SE of Cape Lookout (34°20′ N; 76°12′ W), in 22 fathoms. FLORIDA: 3½ miles NE of Pacific Reef, in 66 fathoms; 2½ miles SSE of Looe Key, in 37 fathoms; Western Dry Rocks; Dry Tortugas (all MCZ). TEXAS: about 68 miles SE of Freeport, in 48 fathoms; about 80 miles S of Port Isabel, in 40 fathoms (both MCZ). CUBA: *Barrera* station 200, Santa Lucia, in 2–4 fathoms; *Barrera* station 208, Bahia Honda, in 1–12 fathoms; *Barrera* station 203, Cabanas Harbor, in 3–12 fathoms (all USNM); Caibarien; Fish Point, Guantánamo Bay (both MCZ). JAMAICA: Green Island Bay; Lucea Bay (both MCZ); Montego Bay (USNM); Port Antonio (MCZ; USNM).

Hispaniola. Haiti: Saltrou (USNM). Puerto Rico: mouth of Anasco River, in 40–60 feet (IMBPR); Mayaguez Harbor, in 10–13 fathoms (USNM; MCZ); La Parguera (MCZ); Salinas Beach, near Guanica (IMBPR); Farjado (MCZ); Johnson Smithsonian Station 75, off Palominas Id., in 26 fathoms (USNM). Lesser Antilles: St. Johns, Antigua, in 5 fathoms (ANSP); English Harbour, Antigua, in 7 fathoms; St. Lucia, in 7 fathoms; St. Lucia, in 10 fathoms; Carlisle Bay, Barbados, in 12 fathoms (all USNM); 2 miles S of Scarborough, Tobago, in 36 fathoms (MCZ).

Tellina (Eurytellina) guildingii *Hanley*

Plate 149, fig. 2; Plate 151, figs. 1–2

Tellina guildingii Hanley 1844, Proc. Zool. Soc. London, **12:** 60 (West Indies); 1846. Thesaurus Conchyliorum, **1:** 230, pl. 56, fig. 1 [type locality, here restricted, White River Beach, Jamaica: holotype, BMNH].

Tellina (*Tellinella*) *guildingii* Hanley. Bertin 1878, Nouvelles Arch. Mus. (2nd series), Paris, **1:** 240.

Tellina (*Tellina*) *guildingii* Hanley. Aguayo y Jaume 1949, Catalogo Moluscos de Cuba, no. 592.

Tellina (*Arcopagia*) *guildingii* Hanley. McLean 1951, New York Acad. Sci., **17**(1): 94.

Description. Shell extending to 53 mm. (about 2 inches) in length and to 30 mm. (about 1¼ inches) in height, elongate-elliptical, thin to subsolid, slightly inequilateral, moderately compressed but with the left valve markedly more convex and with a slight posterior flexure to the right. Umbos just behind the middle, slightly elevated above the hinge line and rather blunt. Anterior margin smoothly and somewhat narrowly rounded; ventral margin straight, rising only slightly posteriorly; anterior dorsal margin gently sloping but stronger in its descent to the anterior dorsal margin; posterior margin more or less straight, at an angle to the dorso-ventral axis and forming an oblique truncation. Sculpture consisting of rather deeply incised, closely set, concentric sulci separated by narrow, crowded bands; radial lirations are variously developed, cover the disc and are

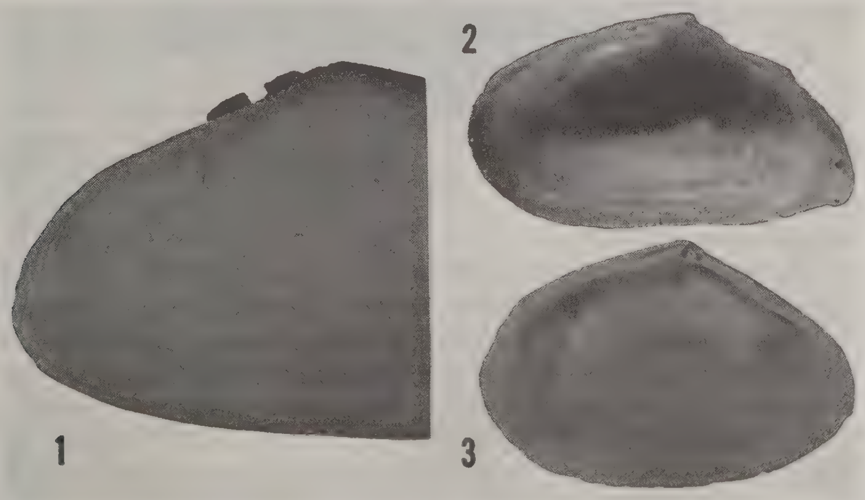

Plate 150. Fig. 1. *Tellina nitens* C. B. Adams, external view of the posterior dorsal slope of the right valve, Lucea Bay, Jamaica, MCZ 212137 (about 4x) [L=about 15 mm.]. Fig. 2. *Tellina vespuciana* d'Orbigny, internal view of the right valve of a syntype, Jamaica, BMNH (about 8.7x) [L=6.5 mm.]. Fig. 3. *Tellina punicea* Born, internal view of the right valve, Guayaguayare Beach, Trinidad, MCZ 236375 (about 1.6x) [L=35 mm.].

more or less absent from the posterior slope and its vicinity. Ligament short, thick, dark to light brown, somewhat protuberant, set in a shallow elongate escutcheon. Calcareous portion of the ligament subtended by a short strong nymphal callosity, especially in the right valve. Hinge moderately well developed. In the left valve, the cardinal complex consists of an anterior, narrow, bifid tooth whose anterior lobe is much the larger and a posterior, thin, laminate tooth which is adpressed to the calcareous portion of the ligament and which is often broken or lost; the anterior lateral tooth is somewhat removed from the cardinal complex, subproximal rather than distal to it and extremely poorly developed; the posterior lateral tooth is distal and variously developed although never strong. In the right valve, the cardinal complex consists of a posterior, strongly skewed, moderately strong, bifid tooth with subequal lobes and an anterior, thickened, well developed subdeltoid laminate tooth; the strong anterior lateral tooth is proximal to the laminate of the cardinal complex; the posterior lateral tooth is distal to the cardinal complex, moderately developed but markedly weaker than the anterior lateral. An internal rib extending from the umbonal area to the anterior adductor muscle scar is well developed in both valves. Adductor muscle scars strongly impressed. Pallial sinus flattened to convex above, extending to and (in younger specimens) coalescing with the anterior adductor scar and falling abruptly with a slight arcuation to the pallial line; confluence entire. Externally, the shell is predominantly white, sometimes with concentric bands of orange or red and usually with radial bands of orange or red which widen peripherally. Inter-

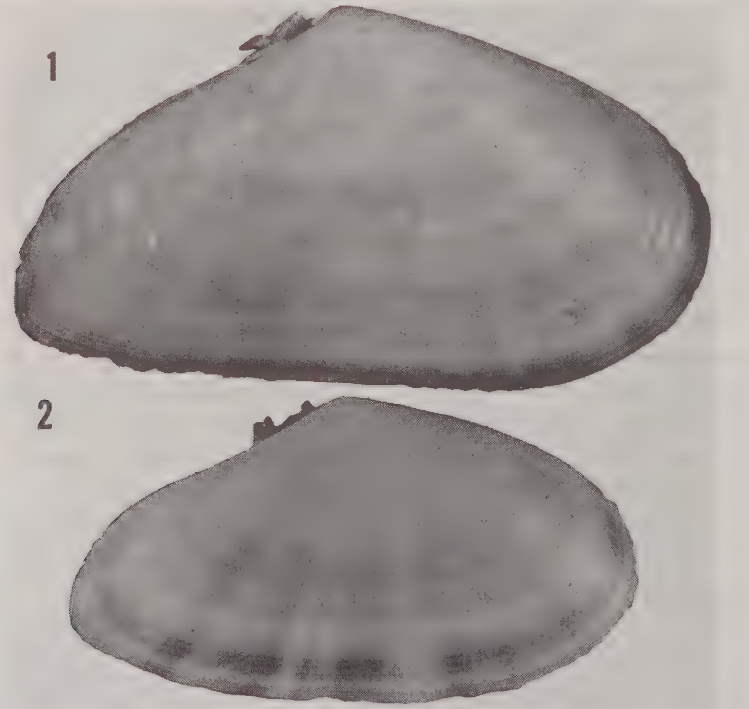

Plate 151. *Tellina guildingii* Hanley. Fig. 1. External view of the right valve of the holotype, West Indies, BMNH (about 3.2x) [L=29.8 mm.]. Fig. 2. External view of the right valve, White River Beach, Jamaica, MCZ 208598 (about 2.4x) [L=34 mm.].

nally, the shell is usually completely white but the transparency of the shell allows the radial and concentric pattern of the external surface to show through.

length	height	width	
29.8 mm.	16.0 mm.	7.0 mm.	Holotype of *guildingii* Hanley
53.5	29.5	—	Bermuda
37.9	29.9	7.8	Rio Bueno, Trelawny, Jamaica
37.4	29.9	7.5	White River Beach, Ocho Rios, Jamaica
34.6	18.2	6.6	White River Beach, Ocho Rios, Jamaica
31.5	14.5	7.5	St. Croix, Virgin Islands

Remarks. This species, as rare as it is and distributed as it is over a wide range, is nevertheless distinct from all the other Western Atlantic *Tellina.* It is not synonymous with *T. nitens* as McLean (1951) has indicated. Of all the Western Atlantic *Eurytellina, nitens* is probably the most closely related species to *guildingii.* The latter, however, is immediately characterized by its concentric sculpture which is strong, deeply incised and closely set; in addition, the peculiar orange sheen of *nitens* is completely lacking in *guildingii,* which instead has a distinctly rayed pattern of coloration. The valves of *guildingii* are heavier and thicker than those of *nitens* and there is no intercalated sculpture on the posterior slope of the right valve. Unfortunately, there is no information as to the habitat preferred by this species. *Tellina waylandvaughani* described by Maury (1917) from the Lower Miocene of Santo Domingo bears some resemblance to the shape and outline of *guildingii.*

Range. This species is rare and poorly represented in museum collections. The Bermuda record from a lot in the MCZ is doubtful, and Peile (1926) does not list this species from there. The lot from Dick's Point, Nassau, New Providence in the Bahamas is also doubtful. It is certain, however, that the species is to be found in Jamaica and that it also probably occurs in the Virgin Islands; such a discontinuous distribution will only be corroborated with further collecting in other Antillean areas.

Specimens examined. BERMUDA: Bermuda (MCZ). BAHAMA ISLANDS: Dick's Point, Nassau, New Providence (MCZ). CUBA: *Atlantis* station 3328, Bahia Cochinas, 22°08′ N: 81°10′ W, in 260–275 fathoms (MCZ). JAMAICA: Rio Bueno, Trelawny (USNM); White River Beach (Yale; USNM; MCZ). VIRGIN ISLANDS: St. Thomas (ANSP); St. Croix (MCZ). LESSER ANTILLES: off Pelican Island in 100 fathoms and in Carlisle Bay in 12 fathoms, both Barbados (both MCZ).

Tellina (Eurytellina) lineata *Turton*

Plate 143, figs. 3–4; Plate 147, figs. 1–2; Plate 149, fig. 3

Tellina striata 'Gmelin' Montagu 1804, Testacea Britannica, pp. 60 and 61, *non* Gmelin 1792, *nec* Spengler 1798, *nec* Costa 1829.

Tellina brasiliana Lamarck 1818, Animaux s. Vertebres, **5:** 532 (l'Océan du Brésil, à Rio de Janeiro) [syntypes, Museum d' Histoire Naturelle, Paris], *non* Spengler 1798.

Tellina lineata Turton 1819, Conch. Dict., p. 168, pl. 4, fig. 16 (coast of Dorsetshire) [type locality, here corrected and restricted, Jamaica; holotype, USNM 172658], *non* Hoeninghaus 1829.

Tellina decussatula C. B. Adams 1845, Proc. Boston Soc. Nat. Hist., **2:** 10 (Jamaica); Clench and Turner 1950, Occ. Papers Moll., Harvard University, **1**(15): 272, pl. 44, figs. 1–2 [lectotype, selected by Clench and Turner, MCZ 156459].

Tellina (*Telinella*) *lineata* Turton. H. and A. Adams 1856, Genera Recent Mollusca, **2**: 395 (error for *Tellinella*).

Tellina (*Tellinella*) *lineata* Turton. Römer 1871, Conchilien-Cabinet (2), **Tellina, 10**(4): 53, pl. 15, figs. 8–12.

Tellina decussata Adams. Krebs 1864, West Indian Shells, p. 101 (error for *decussatula*), *non decussata* Lamarck 1818.

Tellina (*Tellina*) *lineata* Turton. Dall 1900, Proc. U.S. Nat. Mus., **23**: 293.

Tellina (*Moerella*) *lineata* Turton. Dautzenberg 1900, Mem. Soc. Zool., Paris, **13**: 261.

Tellina (*Eurytellina*) *lineata* Turton. Dall and Simpson 1901, Bull. U.S. Fish. Commission, **20**(1): 480.

Tellina (*Tellina*) *decussata* Adams. Maury 1920, Bull. American Paleo., **8**(34): 79 (error for *decussatula*).

Description. Shell extending to 38 mm. (about 1½ inches) in length and to 25 mm. (about 1 inch) in height, subtrigonal or elongate-oval, inequilateral, somewhat inflated with both valves of nearly equal convexity and with a marked and sharp flexure to the right. Umbos raised slightly above the hinge line, inflated with a cavity below, pointed, markedly opisthogyrous and located just posterior to the middle. Anterior margin more or less broadly rounded; ventral margin straight or convex and gently rising; anterior dorsal margin convex, short and gently curving; posterior dorsal margin rather steeply sloping; posterior margin more or less straight, short and forming an oblique truncation. Sculpture consisting of rather closely set, weakly incised, concentric sulci separated by narrow and hardly raised bands of irregular breadth. Weak and broad radial lirations cover the disc. Posterior ridge present but generally not too well developed and stronger on the left valve. Ligament generally dark brown, short, broad and sunken into a broad but shallow escutcheon. Calcareous portion of the ligament very much narrowed posteriorly and subtended by a nymphal callosity, which is rather well developed in the right valve. Hinge line well developed. In the left valve, the cardinal complex consists of an anterior, elongate, bifid tooth with subequal lobes and a posterior narrow and weak laminate tooth which is adpressed to the calcareous element of the ligament; the anterior lateral tooth subproximal, weak and obsolete; the posterior lateral tooth distal, slightly stronger than the anterior but still rather poorly developed. In the right valve, the cardinal complex consists of a posterior, skewed, strong, bifid tooth with irregular lobes and an anterior subdeltoid, strong laminate tooth; the anterior lateral tooth is subproximal to the cardinal complex, strong and well developed; the posterior lateral is weaker and distal. A variously developed anterior rib extends from the umbonal area to the anterior adductor scar. Adductor muscle scars well impressed. Pallial sinus convex above, not rising above the adductor muscle scars, extending anteriorly but usually not coalescing with the anterior adductor scar and falling more or less obliquely to the pallial line; confluence entire. Externally, the shell may be pure white to pure pink; in specimens with pink concentrated on the disc, there are evidences of concentric banding of white and pink. Some suffusion of yellow and apricot may also appear. Internally, the shell is white, pink, or a mixture thereof; the marginal borders are generally white.

length	height	width	
25.0 mm.	16.0 mm.	7.5 mm.	Lectotype of *decussatula* Adams
37.5	24.5	11.6	Marco Pass, Florida
35.5	23.0	12.0	Marco Pass, Florida
34.0	24.0	11.5	Marco Pass, Florida
31.5	21.0	8.5	Isla Coche, Venezuela
16.0	10.5	5.0	Cape Sable, Florida

Remarks. The inclusion of Montagu's interpretation of Gmelin's *striata* in the synonymy is made because of Turton's reference to Montagu in the type description of *lineata*, and all later authors have interpreted Montagu's remarks as being descriptive of Turton's *lineata.* Under the synonyms of *T. lineata* Turton, Dall (1900a) listed Conrad's reference to *Tellina tenuis* daCosta in Say's American Conchology; the specimen figured by Conrad later became the type of *Tellina omoia* Ravenel, which is herein treated as a *nomen oblitum* under *Tellina colorata* Dall.

The range of variation within this species is in part responsible for the synonyms cited above. Certainly the most characteristic trait for this species is the strong posterior flexure to the right, which is absent or only poorly developed in other species in the subgenus *Eurytellina.* Dall (1900a) had tentatively placed it within the framework of the subgenus *Tellina*, as interpreted by him. In the present thesis the concept of *Eurytellina* has been broadened to allow inclusion of *T. lineata.* This species posseses a variously developed internal anterior rib which extends between the umbonal area and the scar of the anterior adductor muscle. The anterior lateral tooth in adult specimens is subproximal and in immature and very young specimens, it appears to be distal. The extent and shape of the pallial sinus is also variable, the distance separating the anteriormost border of the sinus and the scar of the anterior adductor muscle is not constant. The sinus may fall straight or obliquely to its union with the pallial line. In color, *lineata* ranges between a pure white and a pure pink with numerous gradations between, including suffusions of yellow and apricot. As far as can be ascertained, this range of coloration is found within any local population and there does not appear to be any clinical phenomenon involved. As indicated by the measurements, the same may be said for the astonishing variation in shape. In similar localities, shells may be markedly subtrigonal, elongate, subquadriform, or subovate; however, in youthful stages, there is a tendency for the shell to appear quadriform in outline. The posterior dorsal slope may incline steeply or gently, the ventral margin may be straight or convex, and the posterior portion of the shell may appear produced, truncated, or bluntly rounded. Nevertheless, the species is well characterized by its adult dentition, the posterior flexure, the subequal convexity of the valves and the rather conspicuously pointed and strongly opisthogyrous umbo.

The affinities of *Tellina lineata* are somewhat obscured, for there are no documented fossil records and no apparent predecessor species (Maury, 1920). In the fauna of the Eastern Pacific, there is no distinct analog and the closest relatives of this species in the Western Atlantic appear to be *T. nitens* and *T. punicea.* The similar placement of the right anterior tooth as well as the configuration of the pallial sinus are indicative of the propinquity of *nitens* and *lineata*, but *nitens* possesses a distinct and distinguishing intercalated sculpture on the posterior slope of the right valve and lacks the tumidity and convexity of *lineata. Tellina punicea* is even more distantly related, for its right anterior lateral tooth is closer to the cardinal complex than that of *lineata.* In addition, it is of a much more elongate shape with lower proportions and the posterior flexure is but poorly developed. It is to be concluded that *T. lineata* stands more or less alone in the Western Atlantic fauna and that even from its nearest relatives it is quite widely divergent and unique.

Certain species may be superficially confused with *Tellina lineata* but each is easily distinguished by close examination. *Tellina tampaensis*, when compared with *lineata*, shows a lack of a developed right posterior lateral tooth and its pallial sinus is distinctly separated from the anterior adductor muscle scar. *Macoma cerina* 'C. B. Adams' Dall appears to have some similarity in outline to *T. lineata* but the former totally lacks lateral teeth.

Range. This species occurs as far north as St. Augustine, Florida; it is found along the coast of the Gulf of Mexico from Florida to Yucatan. It appears to be very rare in the Bahamas. It occurs throughout the Greater and Lesser Antilles, in the Caribbean Sea, along the coast of eastern Central America and northern South America, and along the shores of eastern South America to São Paulo, Brasil.

Specimens examined. FLORIDA: St. Augustine (USNM); Banana River, near Cocoa Beach (MCZ); Jupiter Inlet (ANSP); mouth of St. John's River (USNM); Lake Worth; North Inlet, Palm Beach (both ANSP); Pelican Shoals; Middle Cape and North Cape, Cape Sable; Small Key, 7½ miles NNW of Lostman's River; Plover Key (all MCZ); Lostman's Key (ANSP); Pavilion Key (MCZ); Cape Romano (USNM); Cape Haze; Horse Key, 11½ miles SE of Marco; Caxambas Pass (all MCZ); Marco, in 2 fathoms; Marco Pass (both USNM); Naples (MCZ); Bonita Beach, Bonita Springs (ANSP; MCZ); Big Carlos Pass; Fort Myers Beach (both ANSP); Bunch Beach (D. and N. Schmidt); Punta Rassa (D. and N. Schmidt; ANSP; USNM; MCZ); Tarpon Bay and Blind Pass, Sanibel Id.; Captiva; Charlotte Harbor (all MCZ); Gasparilla Key (USNM); Little Gasparilla Id. (ANSP); Lemon Bay; Sarasota Bay; Pass-a-grille (all MCZ). TEXAS: Port Aransas (MCZ). MEXICO: Veracruz (USNM; MCZ): Isla del Carmen, and near Chenkan, Campeche; Yucatan (all MCZ). GUATEMALA: Puerto Barrios (MCZ). NICARAGUA: (ANSP). BAHAMA ISLANDS: Abaco (ANSP). CUBA: *Barrera* station 209, Santa Rosa, in 3–6 fathoms (USNM); Veradero Beach, Matanzas (MCZ); Playa Larga, Cardenas (CNM); Cayo Frances, and Cayo Conuco, Caibarien; Nicaro, Mayari (all MCZ); Batabano (ANSP); Nueva Gerona, Isla de Pinos (MCZ); Siguanea Bay, and Punta Colombo, Isla de Pinos (both USNM); ½ mile E of La Milpa, Cienfuegos Bay (MCZ); Cienfuegos Harbor; Ensenada de Cochinos, in 100–150 fathoms (both USNM). JAMAICA: Mamee Bay, St. Anne's Parish (MCZ); Old Harbor, St. Catherine; Hunts Bay; Kingston; Palisadoes (all USNM). HISPANIOLA. HAITI: Ile a Vache; Les Cayes; St. Louis de Sud; Aquin; Bizoton (all USNM). SANTO DOMINGO: Santa Barbara de Samana (MCZ). PUERTO RICO: Catano (IMPBR); Cabras Id.; Mayaguez (both USNM); Salinas de Guanica (IMBPR); El Caja de Santiago (USNM). VIRGIN ISLANDS: St. Thomas (USNM). LESSER ANTILLES: Guadeloupe; St. Lucia (both ANSP); Grenada (USNM); Trinidad (MCZ). COLOMBIA: Cartagena (MCZ). VENEZUELA: Isla Coche; Cumana; Margarita Id. (all MCZ). BRASIL: Fortaleza (USNM); Recife; Ilha de Itaparica, Bahia; Vitoria, Espirito Santo (all MCZ); São Sebastião, São Paulo (USNM).

Tellina (Eurytellina) vespuciana *d'Orbigny*

Plate 148, figs. 3–4; Plate 149, fig. 1; Plate 150, fig. 2

Tellina vespuciana d'Orbigny 1842 [*in*] Sagra, Hist. L'Ile Cuba, Atlas, pl. 26, figs. 12–14; 1845, Spanish Text, **5**(2): 305 (Martinica y Jamaica); 1853, French Text, Mollusques, **2**: 254 [type locality, here restricted, Jamaica; syntypes, BMNH 54.10.4.515].

Tellina (*Arcopagia*) *vespuciana* d'Orbigny. McLean 1951, New York Acad. Sci., **17**(1): 93, pl. 19, fig. 5.

Tellina (*Eurytellina*) *vespuciana* d'Orbigny. Warmke and Abbott 1961, Caribbean Seashells, p. 196.

Description. Shell extending to 7.5 mm. in length (about 5/16 inch) and to 4.5 mm. (about 3/16 inch) in height, elongate, subsolid, moderately inflated, with the left valve of markedly greater convexity and with a flexure to the right posteriorly. Umbos posterior to the middle, opisthogyrous, not elevated and pointed. Anterior margin somewhat broadly rounded; ventral margin more or less straight, rising in a gentle arcuation posteriorly; anterior dorsal margin steeply inclined and convex; posterior margin more or less straight and forming a broad truncation. Sculpture consisting of incised concentric sulci separated by narrow, rather flattened bands; the concentric sculpture increasing in strength along the posterior ridge. Ligament yellowish, short and very protuberant. Calcareous portion of ligament supported by short nymphal callosities. In the left valve, the cardinal complex consists of an anterior slightly thickened bifid tooth with subequal lobes and of a posterior very thin, elongate, laminate tooth; no true lateral teeth present. In the right valve, the cardinal complex consists of a posterior, skewed, weak bifid tooth with narrow lobes and of an anterior small, slightly thickened laminate cardinal tooth; anterior lateral tooth proximal, elongate and upcurled; posterior lateral tooth distal, pointed and socketed above. Adductor muscle scars moderately well impressed. Pallial sinus equal in both valves, rising rather abruptly behind, rounded above, gently descending, approaching very near to but not touching the anterior adductor muscle scar and falling in a smooth arcuation to the pallial line; confluence extensive. Color white to pellucid, rarely with a brownish periostracum externally, not rayed or suffused with red; internally somewhat polished.

length	height	width	
6.5 mm.	3.2 mm.	—	Syntype of *vespuciana* d'Orb.
7.5	4.5	—	La Parquera, Puerto Rico
5.6	3.3	1.7 mm.	La Parquera, Puerto Rico
5.0	3.0	1.4	Jamaica

Remarks. Tellina vespuciana is placed within *Eurytellina* because it conforms to the syndrome of characters exhibited by this group. It is unlike all other members of *Eurytellina* in regard to its extremely small size, and in this trait it indicates the relationship between *Eurytellina* and *Angulus.*

Tellina vespuciana is possibly closely allied to *T. nitens* for there is some sculptural similarity between the two species. In contrast to *nitens*, *vespuciana* in its maximum size is less than 10 millimeters in length, the posterior ridge of the right valve is strong, and the shell lacks any orange-apricot coloration. There does not appear to be any direct eurytellinid analog of *vespuciana* in the Eastern Pacific and it is difficult to assign any ancestral status to fossils in the Western Atlantic which resemble *vespuciana.*

Tellina vespuciana bears the closest resemblance to *T. sybaritica.* The convergence exhibited by these two species is so great as to render the subgeneric status of the species questionable. Both are similar in regard to the superficial sculpture and the configuration of the pallial sinus. *T. sybaritica* possesses an obsolete right distal posterior lateral tooth, but in its variation, this structure very closely approaches the strength of the homologous tooth in *T. vespuciana.* Typically the right posterior lateral tooth in *vespuciana* is pointed, socketed above and strong. In addition, *vespuciana* never possesses bright coloration as *sybaritica* does.

Range. This species is so poorly known that the assignment of a definite range is impossible. It is primarily Caribbean; the single record from the Gulf of Mexico, because of its fragmentary nature, is somewhat questionable.

Specimens examined. TEXAS: off Port Isabel, in 50 fathoms (MCZ). BRITISH HONDURAS: Belize and Monkey River (ANSP). GUATEMALA: Puerto Barrios and Livingston (ANSP). JAMAICA: (MCZ). HISPANIOLA. SANTO DOMINGO: Bahia de Samana, in 16–17 fathoms (USNM). PUERTO RICO: Bahia de Añasco; Mayagüez (both MCZ); La Parquera (IMBPR). LESSER ANTILLES: St. Johns, Antigua, in 30 feet (ANSP); Martinique; Gulf of Paria, Trinidad (both MCZ).

Subgenus **Angulus** *Megerle von Mühlfeld*

Angulus Megerle von Mühlfeld 1811, Gesellschaft Naturforschender Freunde Berlin, Magazin, **5**: 47 (type species, *Tellina lanceolata* Gmelin 1791, subsequent designation, Gray 1847, p. 186).

Oudardia Monterosato 1884, Nomenclatura generica e specifica di alcune Conchiglie Mediterranee, Palermo, p. 22 (type-species, *Tellina oudardii* Payraudeau 1826 [$= T.$ *compressa* Brocchi 1814], original designation).

Moerella 'Fischer' Gardner 1928, U.S. Geol. Sur., Prof. Paper 142-E, p. 195, *non* Fischer 1887.

Anbulus Megerle von Mühlfeld. McLean 1951, New York Acad. Sci., **17**(1): 96, error for *Angulus*.

Description. Shell small to medium in size, fragile to solid, ovate to elliptical in shape, with the left valve generally more convex and with a flexure to the right posteriorly. Sculpture primarily concentric and weakly incised over the surface of the valves; rarely differentiated along the posterior dorsal slope. Hinge without lateral dentition in the left valve. Right valve with the anterior lateral tooth adjacent to the cardinal complex and with an obsolete lateral tubercle. Pallial sinus generally extensive, confluent with the pallial line for much of its ventral length.

Various interpretations have been allotted the group *Angulus*. Megerle von Mühlfeld's original discussion includes a truly heterogeneous assemblage of species with some four kinds of *Angulus* delineated. Later, when Gray (1847) designated *Tellina lanceolata* Gmelin of the Philippines as type, the content of the group was diminished. Salisbury (1934) stated that the type designation of Gray served to restrict *Angulus* to only two Recent species; however, five species bearing the name *Angulus* occur in Salisbury's illustrations. With specific reference to the fauna of North America, Gardner (1928) introduced *Moerella* Fischer to replace *Angulus* which had up to that time become widely used in the literature, and Olsson and Harbison (1953) in following the procedure outlined by Gardner have illustrated the type species of both and described *Moerella* as having 'two strong laterals in the right valve.' The problem is the interpretation of the dental structure of *Tellina donacina*, the type species of *Moerella*, and of *T. lanceolata*, the type species of *Angulus*. *Angulus* lacks any left lateral dentition, and the type species does not have a developed right posterior lateral tooth. However, a fold or slight tubercle along the posterior end of the hinge line in the right valve may be discerned. The anterior lateral tooth in the right valve is well developed, upcurled, and shelf-like. On the other hand, *Tellina donacina*, the type of *Moerella*, has a strong right posterior lateral tooth similar to that developed in *Eurytellina*. The shell is heavy and the concentric sculpture strong.

The morphology of the species in the Western Atlantic exhibits a pattern most closely expressed in *Angulus*. Not only is the right posterior lateral tooth poorly developed or obsolete in the Western Atlantic species, but the general shell construction, in terms of thickness and sculpture, also indicates the relationship with the Indo-Pacific species.

It may be concluded that the anguloid syndrome consists of a right anterior lateral tooth adjacent to the cardinal complex and of an obsolete, absent or poorly developed right distal posterior tooth. The subgenus as herein defined is cosmopolitan in its distribution but with a primary concentration and development of species in the tropics. The group is represented as early as the Eocene in North America.

KEY TO THE SPECIES OF *ANGULUS* IN THE WESTERN ATLANTIC

1.	Shell of high proportions, height more than 70% of length	2
	Shell of lower proportions, height less than 70% of length	5
2.	Shell rounded or ovate in outline; not highly colored	3
	Shell subquadrate in outline; highly colored	*colorata*
3.	Shell with the right anterior lateral tooth subproximal to the cardinal complex	4
	Shell with the right anterior lateral tooth closely adjacent to the cardinal complex	*tampaensis*
4.	Pallial sinus uniting with the pallial line some distance from the anterior adductor muscle scar	*mera*
	Pallial sinus uniting with the pallial line at or near its junction with the anterior adductor muscle scar	*paramera*
5.	Sculpture consisting of raised concentric lirations	6
	Sculpture consisting of finely incised sulci	7
6.	Shell pellucid, highly colored and sharply flexed	*sybaritica*
	Shell dull white and not sharply flexed	*tenella*
7.	Shell solid, subtrigonal and pointed behind	8
	Shell thin to subsolid and elongate-elliptical	9
8.	Posterior slope sharply cleft by a radial sulcus; periostracum grayish-green	*gibber*
	Posterior slope not cleft by a single radial sulcus; shell mostly red in color	*exerythra*
9.	Pallial sinus separated from the anterior adductor muscle scar by at least one millimeter	10
	Pallial sinus closely approaching the anterior adductor muscle scar, separated by less than one millimeter	13
10.	Anterior dorsal margin nearly parallel with the ventral margin, distinctly separated from the anterior margin; shell vitreous	*euvitrea*
	Anterior dorsal margin gently inclined, somewhat convex and not parallel with the ventral margin	11
11.	Shell greatly inflated; right posterior bifid cardinal skewed	*diantha*
	Shell not greatly inflated; right posterior bifid cardinal tooth not strongly skewed	12
12.	Shell compressed; flesh-color with rays posteriorly	*probrina*
	Shell not compressed; white or pink in color	*agilis*
13.	Sculpture along the posterior dorsal slope of the right valve differentiated; often rayed with pink or red posteriorly	*versicolor*
	Sculpture along the posterior dorsal slope of the right valve not differentiated; white to pellucid yellow in color; not rayed posteriorly	*texana*

Tellina (Angulus) tampaensis *Conrad*

Plate 152, fig. 3; Plate 153, fig. 4

Tellina tampaensis Conrad 1866, American Jour. Conchology, **2:** 281, pl. 15, fig. 8 (Tampa Bay, Florida) [syntypes, ANSP 52434].

Tellina (*Angulus*) *tampaensis* Conrad. Dall 1900, Proc. U.S. Nat. Mus., **23:** 296.

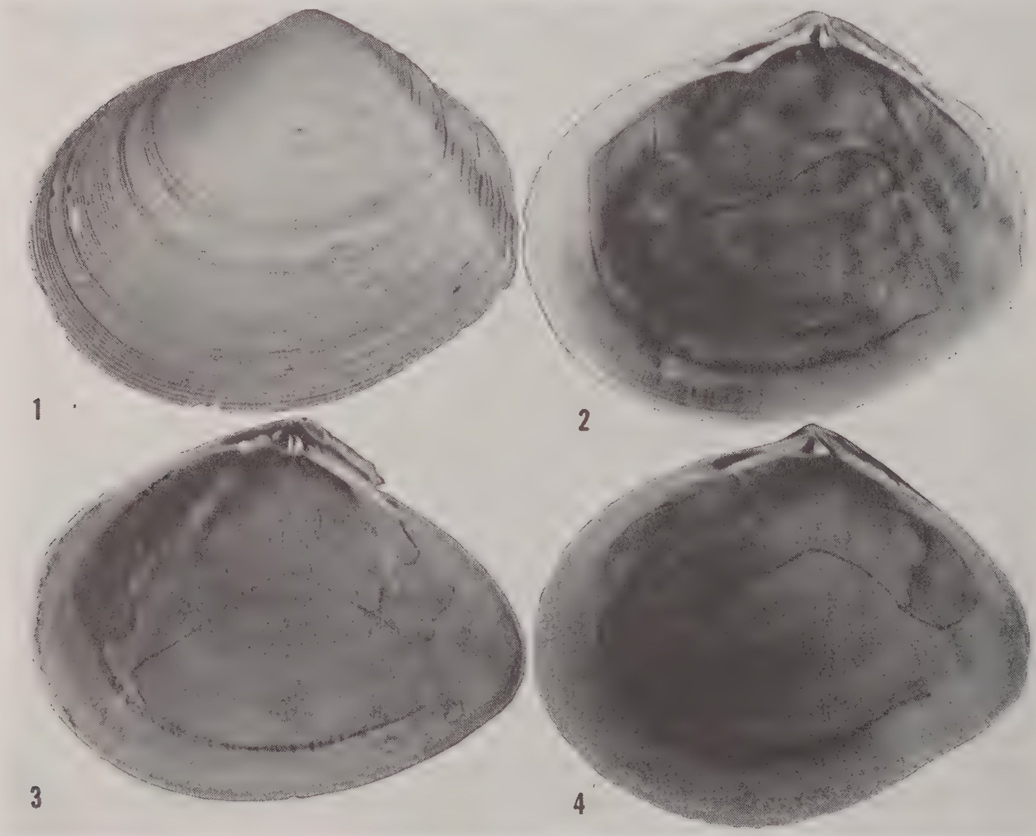

Plate 152. Figs. 1–2. *Tellina paramera* Boss. Fig. 1. External view of the left valve of the holotype. Fig. 2. Internal view of the right valve of the holotype, off Miami Beach, Florida, MCZ 242904 (about 5.6x) [L = 12.5 mm.]. Fig. 3. *Tellina tampaensis* Conrad, internal view of the right valve, Tampa Bay, Florida, MCZ 59480 (about 4.2x) [L = 16.5 mm.]. Fig. 4. *Tellina mera* Say, internal view of the right valve, Madera Bay, Florida, MCZ 236461 (about 4.8x) [L = 15 mm.].

Description. Shell extending to 24 mm. (about 1 inch) in length and to about 18 mm. (about $\frac{3}{4}$ inch) in height, ovate-subtrigonal, produced posteriorly, with the left valve slightly more convex and with a strong posterior flexure to the right. Umbos central and pointed. Anterior margin broadly rounded; ventral margin convex and with a postbasal arcuation; anterior dorsal margin short and gently sloping; posterior dorsal margin steeply sloping; posterior margin short and slightly truncate. Sculpture consisting of concentric lirations separated by narrow, well incised sulci. Ligament brown and protuberant. Calcareous portion of the ligament well developed and subtended by weak nymphal callosities. In the left valve, the cardinal complex consists of an anterior subdeltoid bifid tooth, the anterior lobe being the larger, and of a posterior thickened laminate tooth; no true lateral teeth present. In the right valve, the cardinal complex consists of a posterior skewed, subdeltoid bifid tooth with subequal lobes and of an anterior strong laminate tooth; anterior lateral tooth thin and very close to the cardinal complex; posterior lateral tooth distal and obsolete. Adductor muscle scars well impressed. Anterior adductor longer, narrower and higher than the posterior adductor. Pallial sinus generally similar in both valves, descending to the pallial line in a characteristic short, straight drop and becoming confluent with it some distance from the adductor scar. Externally, shell white, smooth, sometimes iridescent and rarely suffused with a pale peach coloration. Internally, white, shining and often chalky.

length	height	width	
24.0 mm.	18.0 mm.	8.0 mm.	Key West, Florida
18.5	13.5	6.0	Key West, Florida
16.6	17.3	5.7	Tampa Bay, Florida
14.6	11.4	5.0	Tampa Bay, Florida
11.0	9.0	4.5	Trout Bayou, Texas

Remarks. In the Western Atlantic, there are two other species which are closely related and sometimes rather easily confused with *tampaensis. Tellina mera* Say may be differentiated by its right anterior lateral tooth which is more distally removed from the cardinal complex than the same structure in *tampaensis;* furthermore, the pallial sinus in *mera* has only a short posterior confluence with the pallial line. *Tellina paramera* is a heavier and more thickly shelled species; its color is usually pure white and unlike the peach coloration found in *tampaensis.* The anterior lateral tooth of *paramera* though subproximal to the cardinal complex is trigonal, heavy and strong, and the pallial sinus connects directly to the pallial line just beneath the anterior adductor muscle scar.

Tellina tampaensis appears to be related to *Tellina suffusa* of the Eastern Pacific which is distinguished by its unusually large lunular area. In the Indo-Pacific, certain highly colored species, including *Tellina rutila* Dunker from Japan, are very similar to *tampaensis.*

Dall (1900b) listed this species as occurring in the Pliocene marls of the Caloosahatchie River, Florida. The species appears to prefer sandy substrates in shallow water; the maximum depth record is twenty feet.

Range. Tellina tampaensis is found as far north along the Atlantic coast of Florida as Mosquito Lagoon. It is found all along the Gulf coast of Florida and the southern states to Port Isabel, Texas and has been recorded from Jamaica and Haiti.

Specimens examined. FLORIDA: Mosquito Lagoon, near Haulover; Banana River; Lake Worth; Coconut Grove; Biscayne Bay; Madeira Bay (all MCZ); Key Largo; Big Pine Key (both USNM); Boca Chica Key; Key West (both ANSP); Boca Grande Key; Eagle Key; Punta Rassa; Blind Pass and Tarpon Bay, Sanibel (all MCZ); Charlotte Harbor; Useppa Island; Little Gasparilla (all MCZ); Lemon Bay; Sarasota Key; Mullet Key; Gulfport; Tampa Bay (all MCZ); St. Andrew's Bay; Pensacola (both USNM). TEXAS: Espiritu Santo Bay (ANSP); Kellers Bay; Matagorda Bay (both USNM); Trout Bayou, Rockport; Corpus Christi; Port Isabel (all MCZ). BAHAMA ISLANDS: Nassau, New Providence (ANSP). JAMAICA: Montego Bay; Old Harbor, St. Catherine (both ANSP). HISPANIOLA. HAITI: Aquin (USNM).

Tellina (Angulus) mera *Say*

Plate 152, fig. 4; Plate 153, fig. 1

Tellina mera Say 1834, American Conchology, **7:** pl. 64, fig. 2 (coast of South Carolina) [type locality, here corrected and restricted, Bermuda; types lost].

Tellina obtusa Sowerby 1868 [*in*] Reeve, Conch. Icon., **17, Tellina,** pl. 46, fig. 271 (Isle of St. Thomas) [holotype, BMNH], *non* Sowerby 1817.

Tellina (*Angulus*) *mera* Say. H. and A. Adams 1856, Genera Recent Mollusca, **2:** 397.

Tellina (*Angulus*) *promera* Dall 1900, Proc. U.S. Nat. Mus., **23:** 296, pl. 2, fig. 11 (Bermuda) [holotype, USNM 94465].

Tellina (*Angulus*) *obtusa* Sowerby. Salisbury 1934, Proc. Malac. Soc., London, **21**(2): 85, pl. 12, fig. 4.

Tellina (*Angulus*) *guadeloupensis* [*sic*] 'd'Orbigny' Abbott 1958, Acad. Nat. Sci., Philadelphia, Monograph 11, p. 134, pls. 5a–b, Map 8, *non* d'Orbigny 1842.

Description. Shell extending to 25.5 mm. (about 1 inch) in length and to 21.5 mm. (about $\frac{7}{8}$ inch) in height, subovate, sometimes produced posteriorly, thin to subsolid, inflated, with both valves of more or less equal convexity and with a short and sharp posterior flexure to the right. Umbos posterior to the middle, conspicuous and rather pointed. Anterior margin broadly rounded; ventral margin convex and rising posteriorly; anterior dorsal margin gently sloping and concave; posterior dorsal margin steeply inclined and straight; posterior margin parallel to the dorso-ventral axis and forming a blunt truncation. Concentric sculpture consisting of irregularly spaced lirations; radial sculpture weak. Ligament yellowish brown, weak and short. Calcareous portion of the ligament moderately developed; no nymphal callosities. In the left valve, the cardinal complex consists of an anterior subdeltoid bifid tooth with subequal lobes and of a posterior small and thin laminate tooth; no true laterals present. In the right valve, the cardinal complex consists of a posterior, slightly skewed and elongate bifid tooth and of an anterior subdeltoid laminate tooth; anterior lateral tooth subproximal to the cardinal complex and laminate; posterior lateral tooth absent or obsolete. Adductor muscle scars generally well impressed. Anterior adductor elongate and with irregular margins; posterior adductor small and subquadrate. Pallial sinus equal in opposite valves, rising abruptly behind, descending gently toward the anterior adductor scar, but not touching it. The sinus is broadly rounded in front and parallel to the pallial line for some distance before becoming confluent with it. Shell white, shining and rarely iridescent.

length	height	width	
14.5	11.0 mm.	6.6 mm.	Holotype of *obtusa* Sowerby
18.0	14.5	7.0	Holotype of *promera* Dall
25.5	21.0	—	New Providence, Bahamas
19.5	16.0	9.0	St. George's Island, Bermuda
12.0	10.0	5.0	Watling Island, Bahamas

Remarks. The holotype of *Tellina mera* Say which came originally from the Ravenel Collection is apparently lost; it is neither in the Academy of Natural Science, Philadelphia nor in the Charleston Museum; no original measurements were included. The type locality was given as 'the coast of South Carolina' and is erroneous; it is herein corrected to 'Bermuda', which is the type locality of one of the synonyms.

Tellina mera may be immediately distinguished from its closest relatives by the nature of the pallial sinus. This character is diagnostic and separates *T. tampaensis* and *T. paramera* from *T. mera.* The recently described *T. paramera* is the nearest relative of *mera* in the Western Atlantic. The pallial sinus of *paramera* extends to the anterior adductor muscle scar and unites with the pallial line at the base of that scar; the confluence of the pallial sinus with the pallial line is complete and extensive. In *mera*, the sinus is confluent with the pallial line posteriorly and is not coalescent with the anterior adductor muscle scar.

Tellina mera, as presently recognized, possesses an extraordinary degree of variation. Dall proposed the specific name *promera*, which he considered to be a very close relative of *mera*. A review of specimens in major museum collections and a critical examination of Dall's types show that *promera* is a synonym of *mera*. Dall indicated that sculptural differences could separate *promera* from *mera* although the sculptural pattern might be worn away. Such an unstable trait certainly fails in the practical aspects of specific identification and can, therefore, be of little use. Some specimens possess distinct, widely spaced and strong concentric ridges whereas others, at the opposite extreme, are sculptureless, smooth and shining. The range of intermediates representing the whole continuum from sculptureless to heavily ridged may be sampled in a single population. The thickness of the shell also varies between two great extremes; some specimens are fragile and vitreous while others are heavy, solid, and chalky. In conclusion, *mera* is an extremely variable species with numerous plastic characteristics but with certain sufficiently stable, diagnostic traits which form a distinguishably valid syndrome of characters by which the species is recognized.

The Eastern Pacific analog of *Tellina mera* is *T. meropsis* Dall (=*paziana* Dall) which, according to Olsson (1961), is found from California to Ecuador.

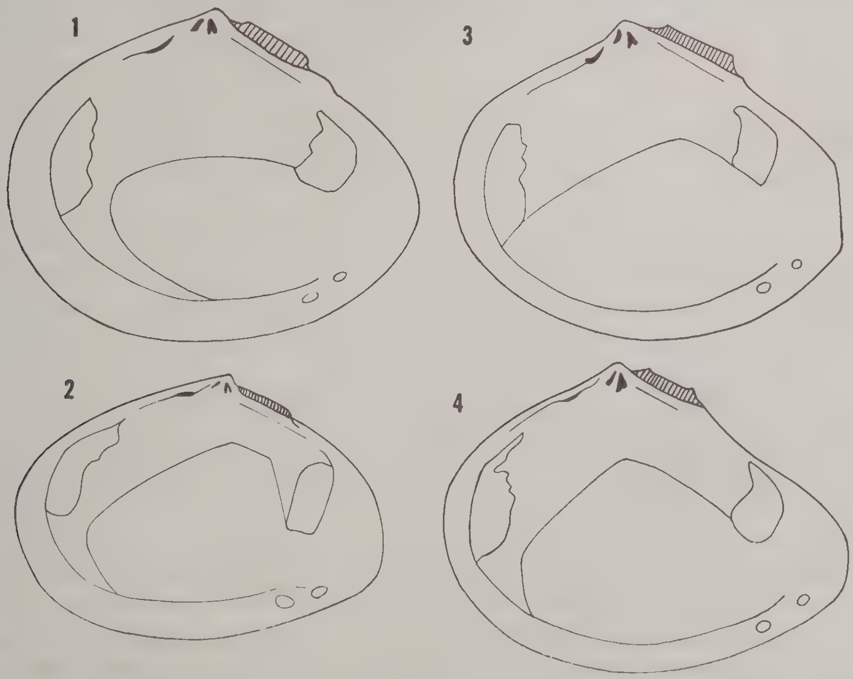

Plate 153. Figs. 1–4. Diagrammatic illustration of the internal surface of the right valve showing the dental configuration and muscle scars. Fig. 1. *Tellina mera* Say (about 4x) [L=15 mm.]. Fig. 2. *Tellina colorata* Dall (about 4x) [L=13 mm.]. Fig. 3. *Tellina paramera* Boss (about 4x) [L=15 mm.]. Fig. 4. *Tellina tampaensis* Conrad (about 4x) [L=15 mm.].

Range. Tellina mera is found from Florida and Bermuda in the north through the Bahama Islands and the Antilles to Barbados and Curaçao.

Specimens examined. FLORIDA: Lake Worth; Ocean Beach; Key Largo; Hawk Channel (all USNM); Lignum Vitae Key (ANSP); Grassy Key; Bonefish Key (both MCZ); Missouri Key; Bahia Honda Key; Sugar Loaf Key; Key West (all ANSP); Barracouda Key; Boca Grande Key; Dry Tortugas; Cape Sable (all USNM); Tarpon Bay, Sanibel; Tampa Bay; Pass-a-grille (all MCZ). BERMUDA: St. George's Island (MCZ); Harrington Sound (USNM). BAHAMA ISLANDS: Little Abaco; New Providence; Cat Island; Watling Island (all MCZ); Great Exuma (USNM). CUBA: Cabo Cajon; Dimas; Santa Lucia; Bahia Honda (all USNM); Cayo Lucas, Las Villas, La Sortiga, Cayo Caiman, and Cayo Salina, Caibarien (all MCZ). HISPANIOLA. SANTO DOMINGO: Puerto Plata; Puerto Sosua (both MCZ). PUERTO RICO: San Juan; Vieques (both USNM). VIRGIN ISLANDS: St. Thomas (ANSP). LESSER ANTILLES: Antigua; Barbados (both USNM). CARIBBEAN ISLANDS: Grand Cayman (ANSP); Curacao USNM).

Tellina (Angulus) paramera *Boss*

Plate 152, figs. 1–2; Plate 153, fig. 3

Tellina (Angulus) paramera Boss 1964, Occ. Pap. Dept. Mollusks, Harvard University, **2**: 311, pl. 55, figs. 3 and 8 (off Miami Beach, Florida, in 8½ fathoms; holotype, MCZ 242904).

Description. Shell extending to 14.5 mm. (about ⅝ inch) in length and to 12.5 mm. (about ½ inch) in height, ovate, subsolid to solid, moderately inflated with both valves of more or less equal convexity and with or without a slight posterior flexure to the right. Umbos posterior to the middle, somewhat elevated, inflated and blunt. Anterior margin broadly rounded; ventral margin convex and rising slightly posteriorly; anterior dorsal margin straight and gently sloping; posterior dorsal margin rather steeply inclined, short and slightly convex; posterior margin short and forming an irregular blunt truncation. Concentric sculpture consisting of closely set, raised ridges (about 8-10 per millimeter) separated by shallow sulci; radial sculpture consisting of poorly developed, evenly spaced lirations which more or less cover the disc. Ligament reddish brown, poorly developed, not protuberant and sunken in an elongate and narrow escutcheon; lunule poorly defined, shallow and broad. Calcareous element of the ligament moderately developed and resting on a flattened hinge plate; no true nymphal callosities. In the left valve, the cardinal complex consists of an anterior deltoid bifid tooth with subequal lobes and of a posterior elongate thickened laminate tooth; no true lateral teeth present. In the right valve, the cardinal complex consists of a posterior, elongate slightly skewed bifid tooth with subequal lobes and of an anterior thickened, subdeltoid laminate tooth; anterior lateral tooth large, strong, thickened and subproximal to the cardinal complex; posterior lateral absent or obsolete, consisting of a weak enlargement in the distal terminus of the hinge plate with an indented socket above. Adductor muscle scars not strongly impressed. Anterior adductor elongate and lunate; posterior scar transversely quadrate. Pallial sinus usually equal in opposite valves, rising abruptly behind, forming a rounded apex above and descending gently to the pallial line below; confluence entire. The pallial sinus generally does not coalesce with the anterior adductor scar but unites with the pallial line just before the anterior adductor scar. Externally, the shell is dull white; internally, shining, not highly polished and tending to become chalky; the internal surface often possesses radial vermiculations which reflect the external radial sculpture.

length	height	width	
12.5 mm.	10.0 mm.	5.2 mm.	Holotype of *paramera* Boss
14.5	12.5	6.5	'Florida Keys'
10.3	8.4	4.3	off Miami, Florida
9.2	7.2	—	off Miami, Florida
6.2	4.5	—	off Miami, Florida

Remarks. This species may be most easily confused with *Tellina mera*, its nearest ally in the fauna of the Western Atlantic. The similarity in shape and color combined with the morphological similarities of the hinge line serve to indicate the close relationship of *mera* and *paramera*. In the latter, however, the shell is noticeably thicker and heavier and, in addition, the posterior margin forms a diagnostic blunt truncation. The configuration of the pallial sinus distinguishes *paramera* from its relatives. In *mera*, the sinus, though extending toward the anterior adductor muscle scar, is separated from it; the sinus then parallels the pallial line for some distance of its ventral length before it falls and unites with it so that the confluence is relatively short. In *paramera*, the pallial sinus is closely aligned to the anterior adductor muscle scar, if not contiguous with it, and the confluence of the pallial sinus with the pallial line is virtually complete, extending the entire ventral length of the pallial line.

Tellina paramera occurs from the shore line to depths of fifty fathoms. Since specimens are relatively rare and the species remained unrecognized until recently, it may be postulated that an offshore habitat in moderate depths is preferred. An analog of *Tellina paramera* does not seem to be recorded for the Eastern Pacific.

Range. The species occurs from Bermuda, through the Bahama Islands and off the coast of southeastern Florida to the Barbados, Lesser Antilles.

Specimens examined. FLORIDA: off Miami Beach, in 6–30 fathoms; off Bear's Cut, Miami, in 18–20 fathoms; off Government Cut, in 3–38 fathoms; off Bell Buoy, Miami, in 15–22 fathoms; off Fowey Light, in 22–40 fathoms; Bird Key, Biscayne Bay, in 2–10 feet (all USNM); off American Shoals, in 45 fathoms (MCZ); Key West; Tortugas, in 15 fathoms (both USNM). BERMUDA: Ferry Point, St. George's Island (USNM). BAHAMA ISLANDS: Grand Bahama (USNM); Thompson's Bay, Long Island (MCZ). CUBA: Cape Cajon; Cayo Levisa; Bahia Honda, in 1–12 fathoms (all USNM). HISPANIOLA. SANTO DOMINGO: Puerto Sosua (MCZ). LESSER ANTILLES: off Payne's Bay Church, in 50 fathoms, and Carlisle Bay, in 6 fathoms, Barbados (both USNM).

Tellina (Angulus) colorata *Dall*

Plate 153, fig. 2; Plate 155, fig. 2

Tellina tenuis 'da Costa' Say 1834, American Conchology, pt. 7, pl. 64, fig. 3.

Tellina omoia Ravenel 1886, Proc. Elliot Soc., **2**(5): 38 (Sullivan's Island, South Carolina) [type lost; *nomen oblitum*].

Tellina (Angulus) colorata Dall 1900, Proc. U.S. Nat. Mus., **23**: 313, pl. 2, fig. 9 (Guadeloupe, Lesser Antilles) [holotype, USNM 42865].

Description. Shell extending to 19.5 mm. (about $\frac{3}{4}$ inch) in length and to 13 mm. (about $\frac{1}{2}$ inch) in height, thin, subquadrate, compressed with the valves of equal convexity and with a weak posterior flexure to the right. Umbos nearly central, small and pointed. Anterior margin narrowly to broadly rounded; ventral margin convex and rising gently posteriorly; anterior dorsal margin long, slightly convex and gently descending; posterior margin forming an oblique truncation. Sculpture consisting of poorly defined, closely set concentric lirations; weak radial lirations also evident. Ligament short, brown and protuberant. Calcareous portion of the ligament well developed and subtended by extremely well developed nymphal callosities. In the left valve, the cardinal complex consists of an anterior subdeltoid bifid tooth with subequal lobes and of a posterior divergent, thin laminate tooth; no true lateral teeth. In the right valve, the cardinal complex consists of a posterior protuberant bifid tooth and of an anterior thickened laminate tooth; anterior lateral tooth immediately proximal to the cardinal complex, thin and laminate; posterior lateral tooth absent or obsolete. Adductor muscle scars well impressed. Anterior adductor narrowly lunate; posterior adductor elongate and quadrate. Pallial sinus more or less equal in opposite valves rising abruptly posteriorly, gently rounded above, well separated from the anterior adductor scar and arcuately descending to unite with the pallial line below; confluence extensive. Externally and internally the shell is smooth and shining, transparent, white and often suffused with apricot, yellow, orange or red.

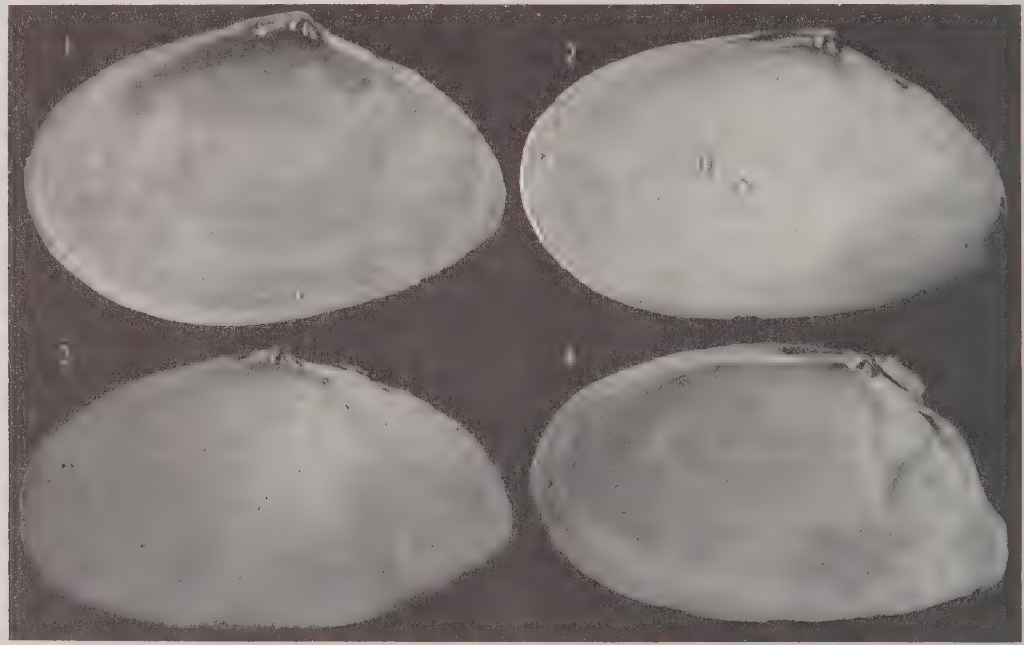

Plate 154. Fig. 1. *Tellina agilis* Stimpson, internal view of the right valve, Revere, Massachusetts, MCZ 230574 (about 4.7x) [L=15 mm.]. Fig. 2. *Tellina texana* Dall, internal view of the right valve, Sanibel Island, Florida, MCZ 53395 (about 6x) [L=12 mm.]. Fig. 3. *Tellina diantha* Boss, internal view of the right valve of the holotype, Barbados, West Indies, MCZ 239110 (about 2.7x) [L=26.5 mm.]. Fig. 4. *Tellina gibber* von Ihering, internal view of the right valve, Puerto Quequen, Argentina, MCZ 118678 (about 4.3x) [L=16 mm.].

length	height	width	
19.5 mm.	13.0 mm.	5.0 mm.	Florida
15.5	11.5	4.0	St. Thomas, Virgin Islands
13.5	9.5	3.8	Guadeloupe, Lesser Antilles

Remarks. This species appears to be very rare and is sporadically dispersed in the Western Atlantic. It does not appear to have an Eastern Pacific analog and is most closely allied to *Tellina tenuis* da Costa of Europe. The similarities between these species are so great and the documentation of living records for *colorata* so poor that some question as to the existence of *colorata* is not unfounded. However, herein *colorata* will be accorded full specific rank until further evidence to the contrary is available. *Tellina colorata* possesses slightly different proportions, being higher and more quadrate with the ventral margin less convex and arcuated than *tenuis.* In addition, the nymphal callosities of *colorata* are more strongly developed, thicker and more protuberant.

Range and specimens examined. Only two lots with specific locality data were available: St. Thomas, Virgin Islands and Guadeloupe, Lesser Antilles (USNM). A lot from Florida (MCZ) is questionable, and specimens from South Carolina are not to be found. At this time no definite range can be stated.

Tellina (Angulus) agilis *Stimpson*

Plate 154, fig. 1; Plate 157, fig. 2

Tellina tenera Say 1822, Jour. Acad. Nat. Sci., Philadelphia, **2:** 303 (inhabits the coast of New Jersey. . . Great Egg Harbor) [syntypes, ANSP 52446], *non* Schrank 1803.

Tellina elucens Mighels 1844 [*teste* Dall 1900], Proc. Boston Soc. Nat. Hist., **1:** 188 (Casco Bay, Maine) [holotype lost; *nomen dubium*].

Tellina (*Angulus*) *tenera* Say. H. and A. Adams 1856, Genera Recent Mollusca, **2:** 398.

Tellina agilis Stimpson 1857, Amer. Jour. Sci., **25:** 125, new name for *tenera* Say.

Angulus tener Say. Verrill 1872, Amer. Jour. Sci., **3:** 290, pl. 6, 1–1a.

Description. Shell extending to 16 mm. (about $\frac{5}{8}$ inch) in length and to 10 mm. (about $\frac{3}{8}$ inch) in height, elongate-subquadrate, rather fragile, somewhat compressed with the valves of more or less equal convexity and with a slight posterior flexure to the right. Umbos posterior to the middle, small and blunt. Anterior margin narrowly rounded; ventral margin gently convex and rising posteriorly; anterior dorsal margin elongate and gently inclined; posterior dorsal margin steeply inclined and short; posterior margin irregular and forming a weakly rounded oblique truncation. Sculpture consisting of weakly incised very closely spaced concentric sulci, imposed on broad growth bands; no true radial sculpture present. Ligament dark yellowish brown, short and slightly protuberant. Calcareous portion of the ligament subtended by weak nymphal callosities. In the left valve, the cardinal complex consists of an anterior subdeltoid bifid tooth with equal lobes and of a posterior thin and elongate laminate tooth; no true lateral teeth. In the right valve, the cardinal complex consists of a posterior, skewed, subdeltoid bifid tooth whose posterior lobe is the larger and of an anterior, thickened laminate tooth; anterior lateral tooth proximal, thickened and often upcurled; posterior lateral tooth distal, weak and obsolete. Adductor muscle scars generally well impressed. Anterior adductor elongate and rounded below; posterior adductor rounded. Pallial sinus more or less equal in opposite valves, arched above, falling with a gentle slope to the pallial line and separated from the anterior adductor. Shell generally white, but rarely suffused with pink or red; interior of valves generally not shining, but of a dull powdery lustre.

length	height	width	
16.1 mm.	9.3 mm.	3.2 mm.	Revere, Massachusetts
16.0	10.6	4.7	" "
13.3	8.4	3.9	" "
10.5	5.6	2.4	Westerly, Rhode Island
4.5	2.8	1.2	Duxbury, Massachusetts

Remarks. Tellina agilis is the northernmost representative of the genus in the Western Atlantic, being the only species of *Tellina* found north of Cape Cod, Massachusetts. The species possesses an extreme range of variation. Immature specimens from one to five millimeters in size tend to be elongate while the proportions in adults are more subquadrate. The color of the shell is nearly always white, but red and pink colored individuals do occur and the color may be concentrated in bands or concentric areas on the valves.

Tellina agilis is replaced by another common species, *Tellina texana*, in the south, although there is some overlap in their ranges. From *texana*, *agilis* may be distinguished by its thinner valves, its greater compression and its disposition of the pallial sinus. In *agilis*, the pallial sinus is impressed and removed from the anterior adductor muscle scar whereas in *texana*, the sinus is less well impressed, generally not as highly arched, and closer to, but not coextensive with the anterior adductor muscle scar. The umbonal sculpture of *texana* is sharp, distinct and slightly intercalated posteriorly, that of *agilis* is smooth, tending to be worn and not intercalated.

Another species related to *Tellina agilis* and often confused with it is *Tellina tenella* Verrill, which because of its rarity has scarcely been documented in the literature. Johnson (1932) has discussed in some detail the traits which separate *tenella* from *agilis*. The outline of *tenella* is distinguished by its narrowly rounded anterior margin, convexly truncate posterior margin and its elongate, slightly concave anterior dorsal margin. Although the umbos are more highly elevated, the general proportions of *tenella* are lower than those of *agilis*. The sculpture in *tenella* consists of lirations separated by well incised sulci which are quite broadly spaced whereas the sculpture of *agilis* consists of very weak, obsolete, closely spaced and fine sulci.

Macoma phenax Dall closely approaches the shape and smooth sculpture of *agilis*, but the former is distinguished by its lack of lateral dentition.

Range. This species is found along the eastern coast of North America from the Gulf of St. Lawrence in the north to Sapelo Island, Georgia in the south.

Specimens examined. CANADA: Gulf of St. Lawrence, in 40–45 meters (USNM); North Ingoish, Cape Breton Island; Ellerslie and Bideford River, Prince Edward Island; Pugwash and East Jeddore, Nova Scotia (all MCZ); Barrington and Three Fathoms Harbour, Nova Scotia (both CNM). MAINE: Quahog Bay; Cushing (both MCZ); Casco Bay; Scarboro (both USNM); Old Orchard (ANSP). MASSACHUSETTS: Ipswich; Annisquam; Danvers; Salem; Marblehead; King's Beach, Swampscott; Lynn Beach; Nahant; Revere; Chelsea (all MCZ); Cohasset; Sam Winsor's Flat, Duxbury (both USNM); Plymouth, in 2–3 fathoms; Provincetown; Georges Bank (all USNM); South

Harwich Beach; Dennisport (both MCZ); Woods Hole; The Gutters, Naushon (both USNM); Five Fingered Point, Eel Point, East Jetty and Wyers Point, Nantucket; Katama Bay, Martha's Vineyard (all MCZ); S of Gay Head; N of Noman's Land; Buzzards Bay (all USNM); Swifts Beach, Wareham; New Bedford; Horseneck Beach (all MCZ). RHODE ISLAND: off Sakonnet, in 5 fathoms; off Newport, in 13 fathoms; Narraganset Bay; Canonicut Island (all USNM); Quonocontave Pond; Noyes Beach (both MCZ); Westerly (USNM). CONNECTICUT: Stonington; Noank (both USNM); Branford (MCZ). NEW YORK: Orient, Peconic Bay and Saybrook, Long Island (all USNM); Far Rockaway Bay, Great South Bay, Point o'Woods, Fire Island Beach and Cold Spring Harbor, Long Island (all MCZ); NEW JERSEY: Point Pleasant; Atlantic City; Norbury's Landing; Holgate, Ocean City; Wildwood (all ANSP); Cape May (CM). DELAWARE: Brandywine Shoal, Old Bare Shoal, Prime Hook Creek, Brown Shoal and Broadkill Creek, Delaware Bay; off Henlopen, in 25 fathoms; 8 miles E of Rehoboth, in 17 fathoms (all USNM). MARYLAND: Plum Point (MCZ); Crisfield; Chesapeake Bay (both USNM). VIRGINIA: Chincoteague (USNM). NORTH CAROLINA: off New Bern (USNM); Smiths Island, Cape Fear (ANSP). SOUTH CAROLINA: Isle of Palms; Folly Island (both CM). GEORGIA: Deboy Channel, Sapelo Island (MCZ).

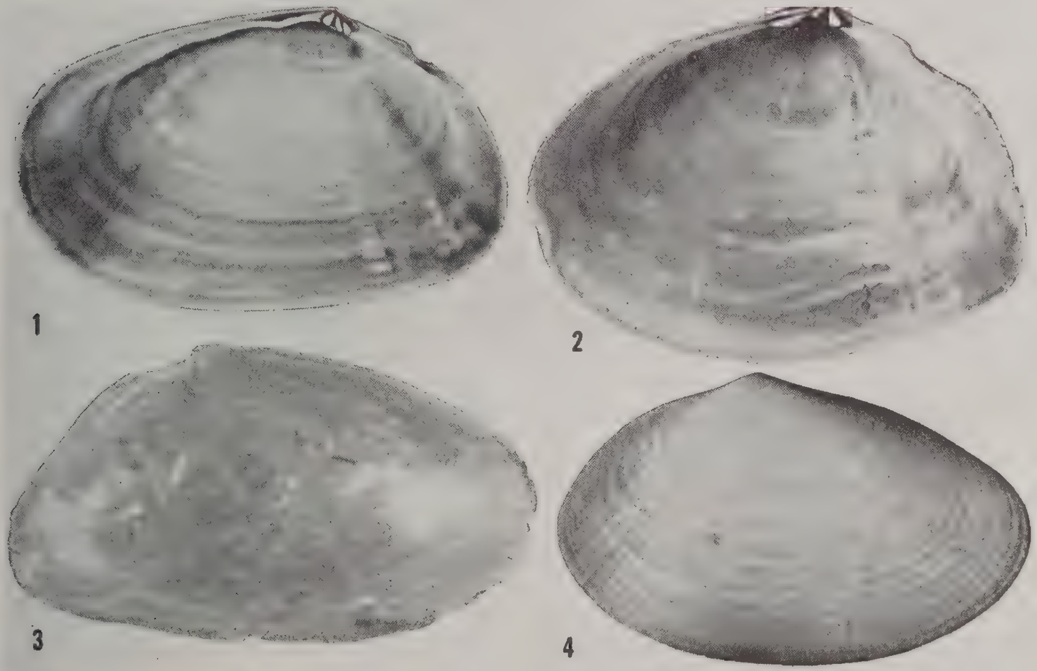

Plate 155. Fig. 1. *Tellina probrina* Boss, internal view of the right valve of the holotype, off Fowey Light, Florida, USNM 461905 (about 4x) [L=18.5 mm.]. Fig. 2. *Tellina colorata* Dall, internal view of the right valve, 'Florida', MCZ 239111 (about 4.8x) [L=15 mm.]. Fig. 3. *Tellina pauperata* d'Orbigny [=*Tellina versicolor* DeKay], external view of the right valve of a paratype, Martinique, BMNH (about 13x) [L=5.8 mm.]. Fig. 4. *Tellina americana* Dall, external view of the right valve, Lantana, Florida, MCZ 208587 (about 10x) [L=6.9 mm.].

Tellina (Angulus) texana *Dall*

Plate 154, fig. 2; Plate 157, fig. 6

Tellina polita Say 1822, Jour. Acad. Nat. Sci., Philadelphia, **2**: 276; 1834, American Conchology, pt 7, pl. 65 fig. 2 (inhabits the southern coast . . . South Carolina and N. Florida) [type locality, here restricted, Charleston, South Carolina; syntypes, ANSP], *non* Poli 1795, *nec* Spengler 1798, *nec* Pulteney 1799.

Angulus polita Say. H. and A. Adams 1856, Genera Recent Mollusca, **2**: 398.

Tellina (*Angulus*) *texana* Dall 1900, Proc. U.S. Nat. Mus., **23**: 295 (Charlotte Harbor, Florida) [holotype, USNM 125539].

Tellina (*Angulus*) *sayi* 'Deshayes MS' Dall 1900, Trans. Wagner Free Inst. Sci., Philadelphia, **3**(5); 1034, new name for *Tellina polita* Say.

Description. Shell extending to 16.5 mm. (about $\frac{5}{8}$ inch) in length and to 9 mm. (about $\frac{3}{8}$ inch) in height, subelliptical to subtrigonal, rather solid, inflated with both valves of equal convexity and with a sharp posterior flexure to the right. Umbos posterior to the middle and blunt. Anterior margin somewhat narrowly rounded; ventral margin straight to convex and rising posteriorly: anterior dorsal margin elongate and gently descending; posterior dorsal margin very elongate and steeply inclined; posterior margin short and forming a blunt end. Sculpture consisting of weak, finely incised, closely spaced concentric sulci; no true radial sculpture. Ligament yellowish brown, strong and protuberant. Calcareous portion of the ligament subtended by protuberant nymphal callosities. In the left valve, the cardinal complex consists of an anterior thickened bifid tooth with subequal lobes and of an elongate posterior laminate tooth; no true lateral teeth. In the right valve, the cardinal complex consists of a posterior skewed thickened bifid tooth with subequal lobes and of an anterior slightly thickened, short, laminate tooth; anterior lateral tooth proximal, thin and slightly upcurled; posterior lateral tooth obsolete and distal. Adductor muscle scars fairly well impressed. Anterior adductor scar elongate and rounded below; posterior adductor scar rounded. Pallial sinus more or less equal in opposite valves, generally convex above, gently inclined and somewhat concave anteriorly and falling arcuately to the pallial line close to but not touching the anterior adductor scar. Shell generally white, sometimes with yellow suffusions. Some iridescence externally and generally highly polished internally.

length	height	width	
16.5 mm.	9.3 mm.	4.8 mm.	Sea Island, Georgia
13.2	7.5	4.2	Port St. Joe, Florida
12.6	6.9	3.8	Grassy Key, Florida
9.8	5.8	3.0	Port Aransas, Texas
6.2	3.6	1.7	Missouri Key, Florida

Remarks. Tellina texana is most closely related to *Tellina agilis* and replaces it along the Atlantic coast of the southeastern states and in the Gulf of Mexico. The range of variation possessed by *texana* is similar in some respects to that of *agilis.* Of the differences which separate *agilis* from *texana*, many have been discussed previously. In *texana*, the valves are more convex, thicker and heavier, the pallial sinus approaches the anterior adductor muscle scar much more closely, and the umbonal sculpture is slightly intercalated. For more extensive comparison of these two species, see *Remarks* under *agilis.*

According to Dall (1900b), *Tellina* (*Angulus*) *declivis* Conrad from the Lower Miocene of Shiloh, New Jersey is very close to *texana*, but the Recent species has a more ventricose shell and the right anterior lateral tooth is longer than in the fossil. Dall also documented the occurrence of *declivis* in the Upper Miocene of Virginia and the Pliocene and Pleistocene of Florida. Richards (1962) has given the Pleistocene records of *T. texana* in North and South Carolina.

Range. This species occurs from North Carolina south through the Bahamas, Florida Keys to Cuba and in the Gulf of Mexico to Progreso, Yucatan.

Specimens examined. NORTH CAROLINA: Beaufort; Pirens Island (both USNM). SOUTH CAROLINA: Isle of Palms; Sullivan's Island (both CM); off Charleston (MCZ); Morris Island (CM); Black Bear Island (MCZ); Porcher's Creek, Porcher's Bluff (CM). GEORGIA: Sea Isle (MCZ); Cumberland Island (CM). FLORIDA: St. Johns River (ANSP); St. Augustine; Palm Beach (both USNM); South Inlet, Lake Worth; Hillsboro Light (both MCZ); Ocean Beach (USNM); Coconut Grove (MCZ); off Miami, in 10 fathoms; SE of Fowey Light, in 25 fathoms (both USNM); Virginia Key (MCZ); Bird Key (USNM); Cards Sound (ANSP); off Caesar's Creek Bank, in 110 feet; off Hawk Channel, in 2–4 fathoms (both USNM); Grassy Key; Missouri Key (both MCZ); Newfound Harbor Key (USNM); Boca Chica Key (MCZ); Key West (USNM); Madeira Bay (MCZ); Marco Island; Bunch Beach (both D. and N. Schmidt); Tarpon Bay and Blind Pass, Sanibel; Punta Gorda (all MCZ); Lemon Bay; Sarasota Bay; Tampa Bay; Gulfport (all ANSP); Pine Island USNM); Seahorse Key and Goose Cove, Cedar Keys; Port St. Joe (all MCZ). TEXAS: Corpus Christi Bay (USNM); off Port Aransas, in 12 fathoms (MCZ). MEXICO: Progreso (ANSP). BAHAMA ISLAND : North side of Abaco (USNM). CUBA: Bahia Honda, in 1–12 fathoms (USNM).

Tellina (Angulus) versicolor *'Cozzens' DeKay*

Plate 155, fig. 3; Plate 156, figs. 1–2; Plate 159, fig. 1

Tellina versicolor Cozzens 1836 [*in*] Jay, Catalog of Shells, 2nd Ed., p. 15 (New York), *nomen nudum.*

Tellina pauperata d'Orbigny 1842 [*in*] Sagra, Hist. L'Ile Cuba, Atlas, pl. 26, figs. 18–20; 1845, Spanish Text, **2**(*5*): 306 (Guadalupe y Martinica); 1853, French Text, Mollusques, **2**: 255 [type locality, here restricted, Martinique; holotype, BMNH 54.10.4.510], *nomen oblitum.*

Tellina versicolor 'Cozzens' DeKay 1843, Nat. Hist. New York, Pt. 1, Zoology, p. 209, pl. 26, fig. 172 (Hudson River at Glass-house Point, New York) [type lost].

Tellina (*Angulus*) *versicolor* 'Cozzens' DeKay. Dall 1900, Proc. U.S. Nat. Mus., **23**: 295.

Tellina (*Angulus*) *pauperata* d'Orbigny. Dall 1900, Proc. U.S. Nat. Mus., **23**: 296.

Description. Shell extending to 17.5 mm. (about $\frac{5}{8}$ inch) in length and to 9 mm. (about $\frac{3}{8}$ inch) in height, elongate, subelliptical, generally thin to fragile, moderately inflated, with both valves of nearly equal convexity and with a posterior flexure to the right. Umbos just posterior to the middle, depressed and pointed. Anterior margin narrowly rounded; ventral margin straight and rising slightly posteriorly; anterior dorsal margin elongate and gently inclined; posterior dorsal margin generally steeply inclined, short and slightly concave; posterior margin long, with a biangulation basally and forming a blunt oblique truncation. Sculpture consisting of widely spaced, strongly incised concentric sulci; no true radial sculpture. Ligament yellowish brown, short, protuberant and subtended by moderately developed nymphal callosities. In the left valve, the cardinal complex consists of an anterior, narrowly elongate bifid tooth and of a posterior thin laminate tooth; no true lateral teeth evident. In the right valve, the cardinal complex consists of a posterior skewed bifid tooth with subequal lobes and of an anterior subdeltoid laminate tooth; the proximal anterior lateral tooth is relatively thin, elongate and upcurled; a weak distal vestige of the posterior lateral tooth is sometimes evident. Adductor muscle scars moderately impressed. Anterior adductor scar elongate and rounded below; posterior adductor scar rounded. Pallial sinus more or less equal in both valves, gently rising posteriorly, convex above and descending arcuately to a fusion with the pallial line below. The sinus comes very close to and sometimes is coextensive with the anterior adductor muscle scar. Color from white to red, translucent to transparent, with variously developed red, pink or white rays which extend radially from the umbo to the postbasal biangulation along the posterior slope. External surface generally shining and iridescent; internal surface polished.

length	height	width	
17.5 mm.	9.0 mm.	—	Santa Rosa, Cuba
13.5	7.5	3.4	Alligator Harbor, Florida
11.0	6.1	3.2	Santa Rosa, Cuba
9.7	5.5	2.1	Chesapeake Bay
6.0	3.0	—	Cape Hatteras, North Carolina

Remarks. The types of *Tellina versicolor* are apparently lost. *Tellina pauperata* d'Orbigny is synonymized herein because its characteristics grade into those of *T. versicolor.* The types of *pauperata* are typically white and pellucid, the posterior slope is very broadly and obliquely truncate, and the posterior dorsal margin is short and strongly concave. Specimens which fit this description occur in populations of *T. versicolor.* In accordance with Article 23b of the Internature Code, *pauperata* is considered as a *nomen oblitum*, or a forgotten name, and *versicolor*, which has been widely used in the literature, is preserved.

The distinguishing characters possessed by *Tellina versicolor* include: 1) its relatively thin, fragile shell; 2) its evenly spaced, incised concentric sculpture with a differentiated area on the posterior slope of the right valve being stronger and nearly lamellose; and 3) its pallial sinus which approaches the anterior adductor muscle scar so closely that at times it appears coextensive with it. Earlier authors considered *T. versicolor* as a species closely related to *T. consobrina*, and the latter was often considered the southern subspecies of the former. However, *Tellina consobrina* possesses a pattern of sculpture which allies it with *Scissula* and it may therefore be quickly separated from *versicolor*. Closely allied to *versicolor* via the placement of the pallial sinus and the thin, fragile nature of the valves is *Tellina probrina* which may be distinguished by its lateral compression, higher, more quadrate proportions and its lack of differentiated posterior slope sculpture.

The species most closely related to *Tellina versicolor* appears to be *T. exerythra.* The characters which identify and distinguish *T. exerythra* as an entity distinct from *T. versicolor* are difficult, if not impossible to quantify, especially at the extremes of variation where overlap occurs and where individual specimens are difficult to place. *Tellina exerythra* is subtrigonal with a thicker shell and higher proportions than *versicolor.* Most specimens of *exerythra* are bright red in color with white peripheral areas. The nature of the pallial sinus, the iridescence of the exterior surface of the valves, the slightly differentiated sculpture of the posterior slope, the incised concentric sculpture on the disc and the presence of red coloration are all traits which indicate the close relationship between *versicolor* and *exerythra.*

Range. This species is found from south of Cape Cod to Trinidad; it occurs in the Gulf of Mexico along the coast of Florida to west Texas.

Specimens examined. Rhode Island: Sakonnet (MCZ). Virginia: Chesapeake Bay, in 3–9 fathoms (USNM). North Carolina: off Cape Hatteras, in 14–48 fathoms; off Cape Lookout, in 18–31 fathoms; Beaufort, in 6–9 fathoms (all USNM). South Carolina: Charleston Harbor (CM). Florida: Banana River; South and North Inlet, Lake Worth; Coconut Grove; Virginia Key; Card Sound; off Elbow, Key Largo; Sombrero Key; Key West; Sand Key; Boca Grande Key (all MCZ); Dry Tortugas (USNM); Marco Island; Punta Rassa (both D. and N. Schmidt); Sanibel; Charlotte Harbor; Sarasota Bay, in 13 fathoms; Bradenton Beach; Gulfport (all MCZ); Sea Horse Key, Cedar Keys; Alligator Harbor (all MCZ); St. Joseph Bay (ANSP); Port St. Joe; Beacon Hill; off Destin, in 14 fathoms; off Fort Walton, in 21 fathoms (all MCZ); Indian Pass, Apalachicola Bay (ANSP). Mississippi: Horn Island (ANSP). Louisiana: Chandeleur Island; Barataria Bay, Grand Isle (both MCZ). Texas: Pass Cabello, Matagorda (USNM); off Port Aransas, in 10 fathoms (MCZ). Mexico: off Cabo Catoche, Yucatan, in 25 fathoms (MCZ). Panama: Mount Hope, Pleistocene (ANSP); Bocas del Toro (Olsson). Cuba: Cape Cajon; Punta Tolete, in 2–3 fathoms; Punta Colorado, in 2–3 fathoms; Dimas, in 4–5 fathoms; Santa Rosa, in 3–6 fathoms; Santa Lucia, in 2–4 fathoms; Esperanza, in 2–3 fathoms; Cayo Arenas, in 2 fathoms; Bahia Honda, in 1–12 fathoms; Cabanas, in 3–12 fathoms (all USNM); Buena Vista Bay, Caibarien (MCZ). Jamaica: Green Island Harbor; Montego Bay; Portland; Little Goat Island, Portland Bight (all USNM). Hispaniola. Haiti: Port au Prince; Les

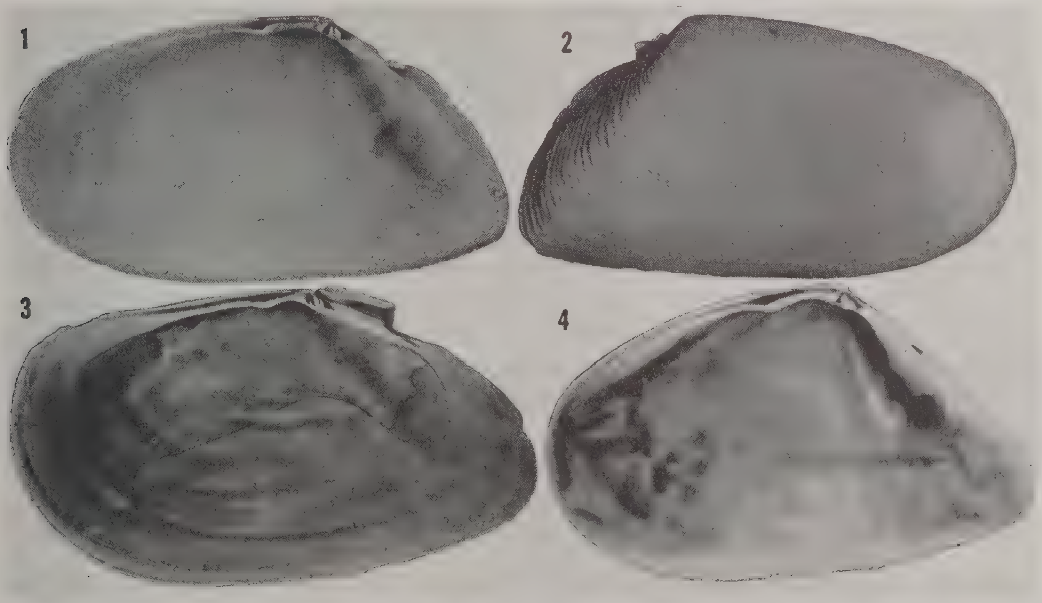

Plate 156. Figs. 1–2. *Tellina versicolor* DeKay. Fig. 1. Internal view of the right valve. Fig. 2. External view of the right valve, Destin, Florida, MCZ 239113 (about 6x) [L = 12 mm.]. Fig. 3. *Tellina euvitrea* Boss, internal view of the right valve of the holotype, Santa Lucia, Cuba, USNM 461952 (about 3.8x) [L = 20.5 mm.]. Fig. 4. *Tellina exerythra* Boss, internal view of the right valve of the holotype, Boca del Infierno, Bahia de Samana, Santo Domingo, MCZ 239220 (about 6x) [L = 12 mm.].

Cayes (both USNM). Santo Domingo: Puerta Plata (MCZ); Samana Bay, in 17–18 fathoms (USNM). Virgin Islands: Charlotte Amelie, St. Thomas, in 30 feet (ANSP). Lesser Antilles: Falmouth Harbor and English Harbor, Antigua, in 3–6 fathoms; Barbados (both USNM); Gulf of Paria, Trinidad (MCZ).

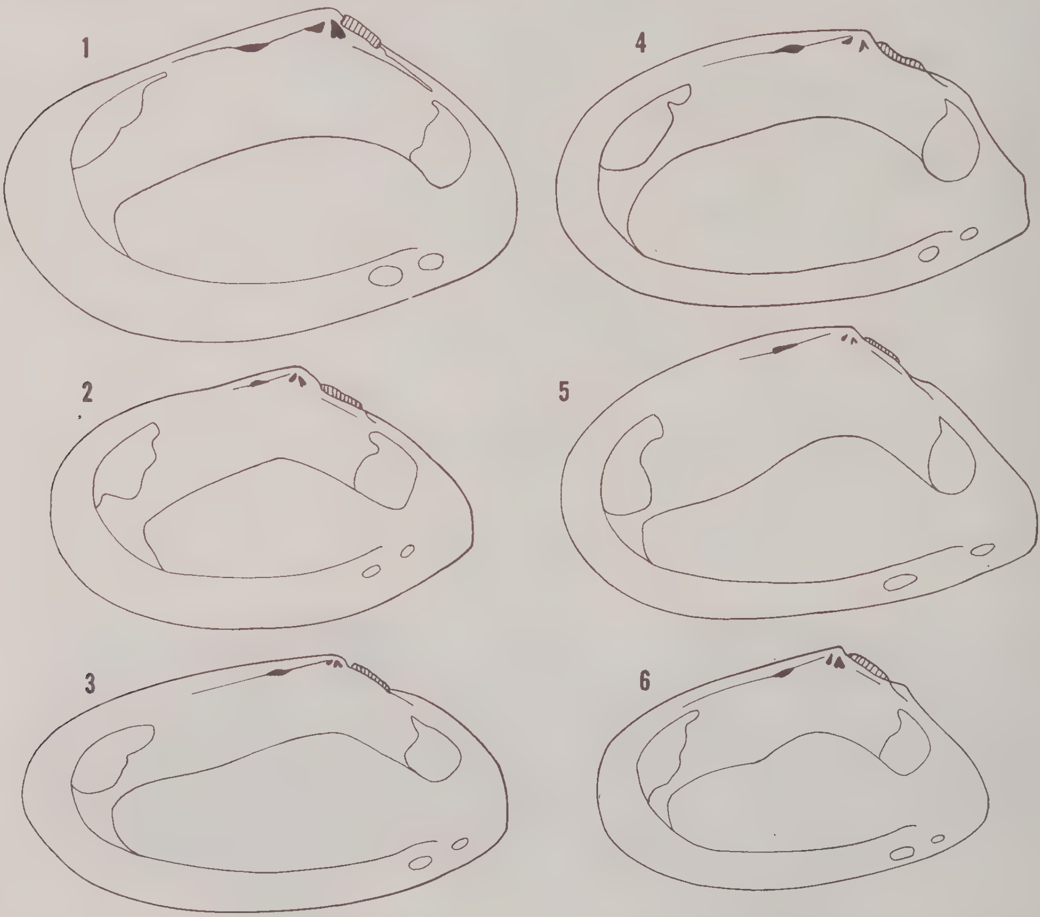

Plate 157. Figs. 1–6. Diagrammatic illustration of the internal surface of the right valve showing the dental configuration and muscle scars. Fig. 1. *Tellina tenella* (Verrill) (about 8x) [L=8.5 mm.]. Fig. 2. *Tellina agilis* Stimpson (about 5x) [L=12.5 mm.]. Fig. 3. *Tellina sybaritica* Dall (about 9x) [L=6.8 mm.]. Fig. 4. *Tellina gibber* von Ihering (about 5.5x) [L=15 mm.]. Fig. 5. *Tellina exerythra* Boss (about 7x) [L=10.3 mm.]. Fig. 6. *Tellina texana* Dall (about 4.4x) [L=13 mm.].

Tellina (Angulus) exerythra *Boss*

Plate 156, fig. 4; Plate 157, fig. 5

Tellina (*Angulus*) *exerythra* Boss 1964, Occ. Pap. Dept. Mollusks, Harvard Univ. **2**: 315, pl. 55, fig. 7 (Boca del Infierno, Bahia de Samana, Santo Domingo, Hispaniola; holotype, MCZ 239220).

Tellina (*Eurytellina*) *vespuciana* 'd'Orbigny' Dall and Simpson 1901, Bull. U.S. Fish. Comm., **20**(1): 480, *non* d'Orbigny 1842.

Description. Shell extending to 18.5 mm. (about $\frac{3}{4}$ inch) in length and to 11 mm. (about $\frac{3}{8}$ inch) in height, subtrigonal, subsolid to solid, inflated with the left valve more convex and with a variously developed posterior flexure to the right. Umbos just posterior to the middle, slightly elevated and pointed. Anterior margin broadly rounded; ventral margin slightly convex and rising in a gentle arcuation posteriorly; anterior dorsal margin elongate and convex; posterior dorsal margin rather steeply inclined and straight; posterior margin short, parallel to the dorso-ventral axis and forming a small truncation. Concentric sculpture consisting of more or less widely and evenly spaced sulci separated by broad, flattened bands; no radial sculpture. Ligament light brown, weak and protuberant. Calcareous portion of the ligament subtended by short and weak nymphal callosities. In the left valve, the cardinal complex consists of an anterior elongate bifid tooth with subequal lobes and of a posterior elongate laminate tooth; no true lateral teeth present. In the right valve, the cardinal complex consists of a posterior, skewed and thickened bifid tooth with subequal lobes and of an anterior subdeltoid laminate tooth; anterior lateral tooth thickened, upcurled and proximal to the cardinal complex; small distal vestige of the posterior lateral tooth evident. Adductor muscle scars moderately impressed. Anterior adductor scar elongate and rounded below; posterior adductor scar rounded. Pallial sinus more or less equal in both valves, rising gently posteriorly, descending in a concave line, extending nearly to but separated from the anterior adductor muscle scar and falling in a short rounded arcuation to the pallial line. Shell basically ivory white in color with a predominance of red suffusion; the periphery is generally white, and variously formed rays of red, white or pink underlie the posterior ridge; external surface shining and sometimes iridescent; internal surface generally highly polished.

length	height	width	
12.0 mm.	7.0 mm.	3.5 mm.	Holotype of *exerythra* Boss
18.3	11.0	—	West Indies
14.8	8.5	—	Santa Barbara de Samana, Santo Domingo
12.8	7.4	3.4	" " " " " "
10.3	6.5	3.0	Mayaguez, Puerto Rico
7.0	4.3	1.9	Bahia de Samana, Santo Domingo

Remarks. Tellina exerythra occurs in considerable numbers in the two easternmost islands of the Greater Antilles. It is most easily confused with and closely related to *T. versicolor.* In general, *exerythra* is subtrigonal in shape, bright red in color and relatively high in proportions. In this respect it can be contrasted with the elongate elliptical shape and whitish coloration of *versicolor.* The shell of *exerythra* is thicker, heavier and of a greater convexity than that of *versicolor.* The posterior ridges of *exerythra* are rather strongly developed, and there are generally one or two supernumerary ridges separated by weak sulci upon the posterior slope. In contrast, *versicolor* possesses less definitively developed posterior ridges, and extra ridges do not seem to be present.

In the south Atlantic, *Tellina gibber,* because of its strong shell and the configuration of its pallial sinus, may be related to *exerythra* but *gibber* lacks the red coloration and possesses a distinctly divided posterior margin with a peculiar and strongly developed posterior sulcus.

Tellina erythronotus Pilsbry and Lowe of the Eastern Pacific is quite similar to *T. exerythra* but the Pacific species attains a greater size.

Range. The species appears to be concentrated in the area of the Greater Antilles exclusive of Cuba. Some specimens have been found at Colón, Panamá and others in Brasil.

Specimens examined. BRITISH HONDURAS: Belize and Monkey River (ANSP). GUATEMALA: Livingston and Puerto Barrios (ANSP). JAMAICA: Little Goat Island, Portland Bight (MCZ). HISPANIOLA. HAITI: Aquin; Bizoton (both USNM). SANTO DOMINGO: Monte Cristi (ANSP); Puerto Plata (MCZ); Matanzas (USNM); Santa Barbara de Samana (MCZ); 3 miles E of Sanchez (USNM); Boca del Infierno (MCZ). PUERTO RICO: Mayaguez (IMBPR; USNM; MCZ); Puerto Real; Cayos Finos, off Ponce (both IMPBR). PANAMÁ: Colón (MCZ); Mt. Hope, Pleistocene (ANSP). BRASIL: Thayer Expedition (MCZ).

Tellina (Angulus) probrina *Boss*

Plate 155, fig. 1; Plate 159, fig. 3

Tellina (*Angulus*) *probrina* Boss 1964, Occ. Pap. Dept. Mollusks, Harvard Univ., **2**: 319, pl. 55, fig. 4 (*Eolis* station 151, off Fowey Light, Florida, in 55 fathoms; holotype, USNM 461905).

Description. Shell extending to 25 mm. (about 1 inch) in length and to 14 mm. (about 9/16 inch) in height, elongate to subrectangular in shape, fragile, compressed, with the left valve of slightly greater convexity and with a slight posterior flexure to the right. Umbos posterior to the middle, small and pointed. Anterior margin broadly rounded; ventral margin straight to slightly convex; anterior dorsal margin long and gently sloping; posterior dorsal margin short, slightly concave and slightly inclined; posterior margin long and forming an oblique and blunt truncation. Sculpture consisting of weakly incised and irregularly spaced, incised concentric sulci; no radial sculpture present. Ligament light brown and protuberant. The calcareous portion of the ligament is subtended by strongly developed and protuberant nymphal callosities in both valves. In the left valve, the cardinal complex consists of a narrow anterior bifid tooth with elongate lobes and of a thin and curved laminate tooth; no true lateral teeth. In the right valve, the cardinal complex consists of a strongly skewed posterior bifid tooth whose posterior lobe is the larger and of an anterior slightly thickened subdeltoid laminate tooth; anterior lateral proximal, laminate and curved upward; posterior lateral absent or obsolete. Adductor muscle scars moderately impressed. Anterior adductor muscle scar irregularly shaped, but elongate and rounded below; posterior adductor more or less rounded. Pallial sinus rising very abruptly from the posterior adductor muscle scar to a high point beneath the umbo, then gently descending, rounded anteriorly and arcuately falling to the pallial line. The pallial sinus is well separated from the anterior adductor muscle scar. Shell white to pink or flesh-colored with a variously shaped posterior ray which may be absent in bleached individuals. The periostracum imparts an iridescence to the external surface of the valves, and the internal surface may be shining.

length	height	width	
18.5 mm.	10.0 mm.	—	Holotype of *probrina* Boss
25.3	14.0	—	off Freeport, Texas
16.0	9.4	—	Bird Key, Florida
14.2	8.4	2.5 mm.	off Fowey Light, Florida
11.1	6.5	2.1	Sombrero Key, Florida
8.3	4.8	—	Bird Key, Florida

Remarks. *Tellina probrina* is most easily recognized by its subrectangular shape and its broad flattened and oblique posterior truncation. Young individuals closely assume the proportions of average adults but very large individuals have the truncation more oblique and the anterior dorsal margin less gently inclined. The vitreous external appearance also identifies this species, but its nearest relative in the Western Atlantic, *Tellina euvitrea*, may be confused with it. However, *euvitrea* has a straight and peculiar anterior dorsal margin, nearly parallel with the ventral margin. In contrast to *probrina*, *euvitrea* is more tumid, much more pointed behind, and the pallial sinus does not rise so abruptly from the posterior adductor muscle scar.

Another species with which *Tellina probrina* may be confused is *T. consobrina;* however, the latter is distinctly allied to *Scissula* and its sculpture may be used to distinguish it from *probrina*. In addition, *probrina* is more compressed, higher in proportions, and more strongly and broadly truncate.

Range. This species occurs in depths up to 100 fathoms. It is found from off North Carolina south to Tobago.

Specimens examined. NORTH CAROLINA: *Eastward* station 1086, 33°42′ N; 76°39.5′ W, S of Cape Lookout, 140–145 meters (MCZ). SOUTH CAROLINA: *Gosnold* station 1403 (M 15), 32°50′ N; 78°18.5′ W, in 140–145 m. (A. Merrill). FLORIDA: off Government Cut, Miami; off Fowey Light; off Ragged Key; off Bird Key; off Triumph Reef (all USNM); off Sombrero Key (MCZ); off Sand Key; Key West; Dry Tortugas (all USNM). TEXAS: 68 miles SE of Freeport, in 48 fathoms; 80–100 miles S of Port Isabel, in 40 fathoms (both MCZ). BAHAMA ISLANDS: (USNM). LESSER ANTILLES: Grenada (USNM); 2 miles S of Fort George, Scarborough, Tobago, in 36 fathoms (MCZ).

Tellina (Angulus) euvitrea *Boss*

Plate 156, figs. 3; Plate 159, fig. 2

Tellina (*Angulus*) *euvitrea* Boss 1964, Occ. Pap. Dept. Mollusks, Harvard Univ., **2**: 321, pl. 55, fig. 5 (*Barrera* station 200, Santa Lucia, Cuba, in 2–4 fathoms; holotype, USNM 461952).

Description. Shell extending to 21 mm. (about 3/4 inch) in length and to 11 mm. (about 7/16 inch) in height, elongate-elliptical, thin, only slightly inflated with the right valve of a greater convexity and with only a slight flexure to the right posteriorly. Umbos just posterior to the middle, opisthogyrous, pointed and not elevated. Anterior margin very broadly rounded; ventral margin straight and with a slight postbasal arcuation; anterior dorsal margin not descending, long, straight and parallel to the ventral margin; posterior dorsal margin variously sloping and short; posterior margin short and poorly defined. Sculpture consisting of weak concentric sulci which are separated by broad bands. Radial sculpture consisting of extremely weak and obscure lirations which are more or less restricted to the peripheral areas. Ligament light brown, strong and protuberant. Calcareous portion of the ligament well developed and subtended by a short nymphal callosity. In the left valve, the cardinal complex consists of an anterior fragile bifid tooth and of a posterior thin and weak laminate tooth; no true lateral teeth present. In the right valve, the cardinal complex consists of a strong posterior bifid tooth with a poorly developed sulcus and of a strong anterior and heavy laminate tooth; no true posterior lateral tooth present; anterior lateral proximal to the cardinal complex, rather small and laminate. Adductor muscle scars generally well impressed. Anterior adductor scar irregularly elongate, smaller than the posterior scar. Pallial sinus equal in opposite valves, pointed above, descending rather steeply and smoothly arcuate anteriorly. The sinus is deep but is well separated from the anterior adductor muscle scar. Externally the shell is iridescent and banded with white or pink; internally, the shell is usually white.

length	height	width	
21.0 mm.	11.0 mm.	4.5 mm.	Holotype of *euvitrea* Boss
20.0	11.0	4.0	Bahia de Samana, Santo Domingo
11.0	6.0	—	Puerto Plata, Santo Domingo

Remarks. This species had actually been recognized by Dall and Simpson in their report on the mollusks of Puerto Rico, and it was at that time called '*Tellina vitrea* d'Orbigny', but the holotype of *vitrea* d'Orbigny is a young individual of *Tellina magna* Spengler. *Tellina euvitrea* is characterized by its periostracum which imparts a vitreous lustre to the external surface of the valves. Its closest relative in the Western Atlantic is *Tellina probrina*, from which *euvitrea* may be separated by a more gently rising pallial sinus, a more pointed posterior end, and by a peculiar anterior dorsal margin which is parallel to the ventral margin. In addition, *Tellina probrina* is compressed whereas *euvitrea* is somewhat inflated. Some individuals of *T. versicolor* may be confused with *euvitrea*, but generally the red coloration and the pallial sinus, which is closely aligned to the anterior adductor muscle scar in *versicolor*, serve to identify it.

Range. This species appears to be more or less restricted to the Greater Antilles except for Jamaica where it has not been recorded.

Specimens examined. CUBA: Santa Lucia, in 2–4 fathoms; La Esperanza, in 4–6 feet; Bahia Honda, in 1–12 fathoms; Cabanas Harbor, in 3–12 fathoms (all USNM). HISPANIOLA. SANTO DOMINGO: Puerto Plata (MCZ); Bahia de Samana (USNM). PUERTO RICO: Aquadilla; mouth of Añasco River, in 40–60 feet (both MCZ); Mayagüez, in 42–60 feet (IMBPR; USNM); off Ponce, in 50 feet (IMBPR).

Tellina (Angulus) diantha *Boss*

Plate 154, fig. 3; Plate 159, fig. 4

Tellina (*Angulus*) *diantha* Boss 1964, Occ. Pap. Dept. Mollusks, Harvard Univ., **2**: 323, pl. 55, fig. 6 (Barbados, British West Indies; holotype, MCZ 239110).

Description. Shell extending to 26 mm. in length (about 1 inch) and to 15 mm. (about $\frac{5}{8}$ inch) in height, elongate-subelliptical, thin, fragile, with the right valve of a greater convexity and with a slight flexure to the right posteriorly. Umbos posterior to the middle, inflated and blunt. Anterior margin generally narrowly rounded; ventral margin straight to slightly convex and rising posteriorly; anterior dorsal margin long and gently sloping; posterior dorsal margin straight and short; posterior margin short and forming a poorly defined, oblique truncation. Sculpture consisting of closely set, weakly developed concentric lines; no true radial sculpture present. Ligament light to dark brown and slightly protuberant. Calcareous portion of the ligament subtended by slightly protuberant nymphal callosities. In the left valve, the cardinal complex consists of an anterior small, subdeltoid bifid tooth with subequal lobes and of a posterior, very thin, extremely elongate laminate tooth; a subproximal anterior lateral thickening represents a vestige of the anterior lateral tooth; no posterior lateral dentition. In the right valve, the cardinal complex consists of a posterior skewed bifid whose posterior lobe is much the larger and of an anterior short slightly thickened laminate tooth; the anterior lateral tooth is proximal to subproximal, thin, laminate and often weakly upcurled; no true lateral tooth present. Adductor muscle scars moderately impressed. Anterior adductor muscle scar narrow and rounded below; posterior adductor scar subquadrate. Pallial sinus more or less the same in opposite valves, rising gently behind, rounded above, descending gently in a more or less straight line and falling in an arcuation to the pallial line; the sinus is distinctly removed from the anterior adductor scar. Externally, shell smooth, shining and suffused with pink or yellowish green; internally, chalky.

length	height	width	
26.5 mm.	15.0 mm.	7.0 mm.	Holotype of *diantha* Boss
23.0	14.0	7.5	Totness, Coronie, Surinam
22.3	13.0	6.4	Rio de Janeiro, Brasil
22.0	13.1	6.0	Belem, Brasil

Remarks. The relationship of this species with others obviously allied to it is obscured by its apparent rarity and the fact that no ontogenetic series of specimens has yet been collected. The large adult size of this species quickly distinguishes it from other members of *Angulus*, but such a character is unsatisfactory as a diagnostic trait. The peculiarly elongate posterior cardinal tooth in the left valve possesses some diagnostic value. In addition, the width and general tumidity of the valves constitutes a further aid in identification.

The closest relatives of this species are *Tellina euvitrea* and *T. probrina.* With respect to both of these species, *diantha* is more tumid and of a different outline, possessing a poorly differentiated posterior truncation and a comparatively shorter anterior dorsal margin. The umbo in *diantha* is more nearly equilateral although still behind the middle and the pallial sinus does not rise abruptly from the posterior adductor muscle scar and extends more anteriorly than in either *euvitrea* or *probrina.*

A fine series of *diantha* has been found by Altena in Surinam. The series from Totness, Coronie, consists of two complete specimens plus five right valves and two left valves. They are designated as paratypes for this species; the specimens are preserved in the Rijksmuseum van Natuurlijke Historie, Leiden.

Range. Although there are only a few records for the species they indicate a rather extensive range, from the Barbados in the Lesser Antilles south to Rio de Janeiro, Brasil.

Specimens examined. Lesser Antilles: Barbados (MCZ). Surinam: Totness, Coronie (Rijksmuseum, Leiden). Brasil: Belem, Para (MCZ); Rio de Janeiro (USNM).

Tellina (Angulus) gibber *von Ihering*

Plate 154, fig. 4; Plate 157, fig. 4

Tellina (Angulus) gibber von Ihering 1907, Anales del museo Nacional de Buenos Aires, 14, Ser. 3a, **7**: 456, pl. 18, figs. 126 a-b (Puerto Militar, Bahia Blanca) [holotype, Museo Nacional de Buenos Aires, Argentina].

Description. Shell extending to 19.5 mm. (about ¾ inch) in length and to 10.5 mm. (about ⅜ inch) in height, elongate-elliptical, fragile to subsolid, rather compressed, with the valves more or less equal in convexity and with little or no posterior flexure. Umbos posterior to the middle and blunt. Anterior margin narrowly rounded; ventral margin rounded in front, convex and rising posteriorly; anterior dorsal margin rather long and more or less straight; posterior dorsal margin often divided into two sections, one a straight and short portion immediately above the hinge line and the other a longer convex posterior portion; posterior margin short and forming a small blunt truncation. Sculpture consisting of regularly spaced, finely incised concentric sulci (about 4–7 per millimeter) separated by broad flattened bands; extremely fine radial lirations may occur on the disc. A posterior ridge and a variously developed sulcus, which bisects the posterior slope, occurs in both valves. In the left valve the cardinal complex consists of an anterior thickened bifid tooth with subequal lobes and of a posterior thin laminate tooth; no true lateral teeth developed. In the right valve, the cardinal complex consists of a posterior subdeltoid, slightly skewed bifid tooth whose posterior lobe is larger and of an anterior thickened subdeltoid laminate tooth; the anterior lateral tooth thin, elongate and proximal to the cardinal complex; the posterior lateral tooth distal, thin and socketed. Adductor muscle scars poorly impressed. Anterior adductor larger, longer and narrower than the posterior. Pallial sinus equal in opposite valves, rising only slightly behind, convex above and descending in an arcuation to the pallial line. The sinus does not touch and is rather widely separated from the anterior adductor scar. Externally, the shell is white, shining and somewhat iridescent; periostracum greenish or brownish; internally, polished and white.

length	height	width	
16.0 mm.	9.5 mm.	4.0 mm.	Holotype of *gibber* von Ihering
19.5	10.5	5.0	off Benninga, Argentina
16.5	9.5	4.5	Puerto Quequen, Argentina
12.5	7.5	3.5	Puerto Quequen, Argentina
9.2	5.0	2.1	La Paloma Rocha, Uruguay
5.0	2.6	—	off Montevideo, Uruguay

Remarks. The character which clearly separates this species is the presence of a sulcus which bisects the posterior slope. The sulcus is variously developed and in some specimens is so strong as to give the shell a constricted appearance. The posterior dorsal slope is also divided into two portions by the sulcus, thereby making the posterior slope appear very short and blunt.

The species is an off-shore dweller and seems to have a preference for depths between 7 and 30 fathoms. The nearest discernible relative is *Tellina hiberna* Hanley of the Eastern Pacific, which compares with *gibber* in the similarity of the peculiar sulcal configuration of the posterior margin and slope; however, *hiberna* is more attenuated posteriorly, the sculpture a little more coarse, the umbo further behind the middle and the shell a bit thinner. *Tellina gibber* was originally described as a fossil and is present in the Tertiary of Argentina and Uruguay (Figueiras, 1962).

Range. This species is strictly southern in its distribution. It is found from off the coast of Uruguay at La Paloma Rocha south along the coast of Argentina to Golfo San Matias.

Specimens examined. URUGUAY: La Paloma Rocha; off Montevideo, in 7 fathoms (both MCZ). Argentina: Puerto Quequen, Buenos Aires; off Cabo Bermeja, off Benninga Head, and off Balem Head, Golfo San Matias, in 17–25 fathoms (all USNM).

Tellina (Angulus) tenella *Verrill*

Plate 157, fig. 1; Plate 158, figs. 3–4

Angulus modesta Verrill 1872, Amer. Jour. Sci., **3**: 211 (typographical error).

Angulus modestus Verrill 1872, Ibid., p. 285, pl. 6, figs. 2–2a (Vineyard Sound, Buzzard's Bay, and Long Island Sound, off New Haven) [syntypes, Peabody Museum, Yale Univ.], *non* Carpenter 1864.

Angulus modestatus Verrill [*in*] Verrill and Smith 1874, Report upon Invert. Animals of Vineyard Sound and Adjacent Waters, p. 124 (typographical error).

Angulus tenellus Verrill [*in*] Verrill and Smith 1874, Ibid., p. 383, pl. 30, fig. 224, *non tenella* Jeffreys 1881, new name for *modestus* Verrill.

Tellina tenella Verrill. Dall 1889, Bull. no. 37, U.S. Nat. Mus., p. 60, pl. 56, fig. 12.

Tellina (*Angulus*) *tenella* Verrill. Dall 1900, Proc. U.S. Nat. Mus., **23**: 295.

Description. Shell extending to 10 mm. (about $\frac{3}{8}$ inch) in length and to 6.4 mm. (about $\frac{1}{4}$ inch) in height, subelliptical, solid, slightly tumid, with both valves of equal convexity and without a posterior flexure. Umbos elevated, small and blunt. Anterior margin narrowly rounded; ventral margin rounded and with a postbasal arcuation; anterior dorsal margin long and concave; posterior dorsal margin steeply inclined, short and concave; posterior margin short, convex and forming a rounded blunt truncation. Sculpture consisting of closely spaced, concentric sulci separated by rounded bands; no true radial sculpture present. Ligament light brown, short and protuberant. Calcareous portion of the ligament not strongly developed; nymphal callosities not prominent. In the left valve, the cardinal complex consists of an anterior small subdeltoid bifid tooth with subequal lobes and of a posterior, short and thin laminate tooth; no lateral teeth present. In the right valve, the cardinal complex consists of a posterior slightly skewed subdeltoid bifid tooth whose posterior lobe is much the larger and of an anterior thickened subdeltoid laminate tooth; anterior lateral tooth proximal to the cardinal complex and thickened; no posterior lateral present. Adductor muscle scars generally well impressed. Anterior adductor scar narrow, subrectangular and rounded below; posterior adductor scar almost perfectly round. Pallial sinus more or less equal in both valves, gently and only slightly rising, convex above, rounded anteriorly and falling in a smooth arcuation to the pallial line. The pallial sinus is distinctly separated from the anterior adductor muscle scar. Interior surface of valves roughened and thick. Color generally white but sometimes brownish or reddish.

length	height	width	
10.0 mm.	6.4 mm.	2.5 mm.	Vineyard Sound, Massachusetts
9.3	6.2	2.5	Woods Hole, Massachusetts
9.0	5.5	2.5	Sanibel Island, Florida
8.2	5.4	2.5	Sarasota, Florida
3.5	2.0	—	off Cape Hatteras, North Carolina

Remarks. Part of the obscurity which has surrounded this specific name was caused by the plethora of errors committed in its original designation and its comparison with *Angulus tener* (*Tellina agilis*). The specific name was first introduced as *Angulus modesta;* the spelling is a typographical error since Verrill used '*modestus*' in the original description. The type figure, pl. 6, figs. 2–2a, is good, but in the text of the description, Verrill refers to pl. 7 (also an error), fig. 1 as that of *modestus* and fig. 2 as that of ***A.** tener* (***T.** agilis*) so unfortunately some workers confused the two.

Tellina tenella is a distinct and somewhat rare species, being originally restricted to the Long Island and Vineyard Sound area in the north; however, its range was greatly extended by Dall (1889) and then later altered by him (1900a). Under the present interpretation, the species extends from the Woods Hole region in the north to the west coast of Florida. Over the extent of this range, a considerable amount of variation is evident. As shown in the descriptive measurements given above, the normal proportions are somewhat altered in the southern populations of *tenella.* With its finely incised, regularly spaced sculpture, *Tellina tenella* is allied to *T. sybaritica* but the latter is much more inflated, more highly colored, flexed behind, and of lower proportions. From *T. agilis*, which is more distantly removed than *T. sybaritica, tenella* may be distinguished by its arcuate ventral margin, its elongate, concave anterior dorsal margin and its shorter and more blunt posterior truncation. In addition, the pallial sinus approaches the anterior adductor muscle scar much more closely in *tenella* than in *agilis. Tellina pygmaea* Philippi of Europe bears some resemblance to *T. tenella*, but the former possesses a more distantly removed right anterior lateral tooth, is more highly colored and of a greater convexity.

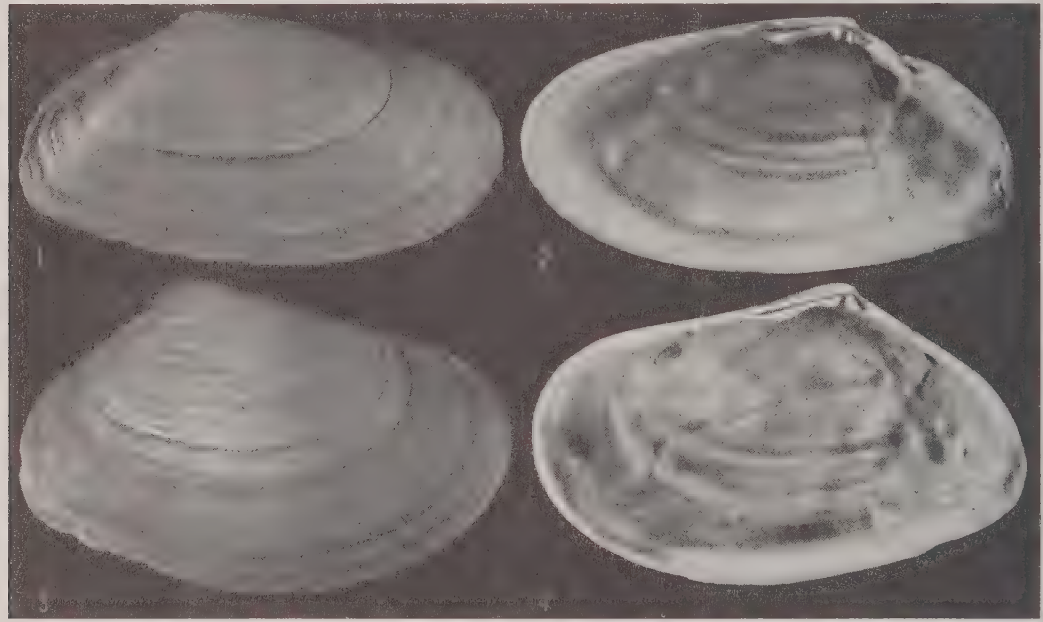

Plate 158. Figs. 1–2. *Tellina sybaritica* Dall. Fig. 1. External view of the right valve. Fig. 2. Internal view of the right valve, off Cabo Catoche, Mexico, USNM 323145 (about 8x) [L=8.5 mm.]. Figs. 3–4. *Tellina tenella* (Verrill). Fig. 3. External view of the right valve. Fig. 4. Internal view of the right valve, Vineyard Sound, Massachusetts, Yale 76973 (about 8x) [L=9 mm.].

Range. This species occurs from Woods Hole to south of Cape Lookout, and in the Gulf of Mexico, it is found along the west coast of Florida to Mississippi.

Specimens examined. Massachusetts: Swift's Beach, Wareham (USNM); Buzzards Bay (ANSP); Woods Hole (USNM; MCZ); off Gay Head Light, in 10–13 fathoms

(USNM); off Martha's Vineyard (ANSP); off Noman's Land (USNM). North Carolina: off Beaufort, in 6–9 fathoms; off Cape Hatteras, in 15–18 fathoms; off Cape Lookout, in 18–31 fathoms (all USNM). Florida: Sanibel (MCZ); Charlotte Harbor; Sarasota Bay (both USNM); Destin (MCZ); St. Josephs Bay; Crooked Island, St. Andrews Sound (both ANSP). Mississippi: Horn Island (ANSP).

Tellina (Angulus) sybaritica *Dall*

Plate 157, fig. 3; Plate 158, figs. 1–2

Tellina sybaritica **Dall 1881, Bull. Mus. Comp. Zool., 9: 134; 1886, Bull. Mus. Comp. Zool., 12(6): 27, pl. 6, fig. 11 (Yucatan Strait, in 640 fathoms) [holotype, USNM 333600].**

Tellina (Angulus) flagellum Dall 1900, Proc. U.S. Nat. Mus., **23**: 312, pl. 2, fig. 6 (off Cape San Roque, Brasil, in 20 fathoms) [holotype, USNM 108534].

Tellina (Angulus) rubricata Perry 1940, Nautilus, **53**(3): 79 (off Blind Pass, Sanibel Island, Florida, in 5 fathoms) [holotype, ANSP].

Description. Shell extending to 11 mm. (about $\frac{3}{8}$ inch) in length and to 5.7 mm. (about $\frac{1}{4}$ inch) in height, elongate, bluntly pointed behind, solid, rather inflated with the left valve of greater convexity and with a posterior flexure to the right. Umbos posterior to the middle, small and pointed. Anterior margin narrowly rounded; ventral margin convex and rising in a gentle arcuation behind; anterior dorsal margin elongate and gently inclined; posterior dorsal margin short and convex; posterior margin irregular, biangulate and forming a produced and blunt truncation. Concentric sculpture consisting of regularly spaced incised sulci separated by rounded lirations; no true radial sculpture. Ligament light brown, strong and set in a shallow escutcheon. Calcareous portion of ligament subtended by weak nymphal callosities. In the left valve, the cardinal complex consists of an anterior narrowly elongate bifid tooth with equal lobes and of a posterior thin, short laminate tooth; no true lateral teeth present. In the right valve, the cardinal complex consists of a posterior skewed, slightly thickened bifid tooth whose posterior lobe is the larger and of an anterior laminate tooth often coextensive with the anterior lateral tooth; anterior lateral tooth proximal to the cardinal complex, thickened and upcurled; posterior lateral tooth obsolete. Adductor muscle scars moderately well impressed, often obscured by the polished internal surface of the valves. Anterior adductor scar elongate to ovate, irregular above, rounded below; posterior adductor scar irregularly subquadrate. Pallial sinus equal in opposite valves, descending in a concave line to and nearly touching the anterior adductor muscle scar and then falling to the pallial line. Basic color predominantly white and suffused with red, yellow, pink or peach; red or pink rays extend postbasally from the umbonal region along the posterior slope.

length	height	width	
10.5 mm.	5.5 mm.	3.7 mm.	Holotype of *sybaritica* Dall
9.0	5.0	3.0	Holotype of *flagellum* Dall
8.0	4.1	—	Holotype of *rubricata* Perry
10.9	5.7	—	Castle Harbour, Bermuda
4.4	2.1	—	Cabo Catoche, Yucatan

Remarks. Tellina sybaritica is typically elongate with a long and slightly convex anterior dorsal margin and a short concave posterior dorsal margin; the posterior margin is irregularly biangulate and obliquely truncated. The shell is solid, thick and strong with a tendency to be highly polished internally; the tumidity of the valves is considerable and distinctive, as is the more or less strong posterior flexure to the right. The sculpture consists of raised rounded ribs or lirations separated by shallow incised sulci, and as Dall noted, this configuration imparts a silky sheen to the surface of the valves.

By its relatively strong sculpture, *Tellina sybaritica* is related to *T. tenella;* however, the latter is distinguished by its lateral compression, its broad, blunt posterior truncation, and its lack of a posterior flexure to the right.

Tellina sybaritica converges with *Tellina vespuciana* d'Orbigny of the subgenus *Eurytellina.* The size, coloration, sculpture and shape of some individuals of these two species are extremely similar. The main trait which differentiates them is the strong development of the distal posterior lateral tooth in the right valve of *vespuciana.* In addition, *vespuciana* seems to possess a finer, intercalated umbonal sculpture and the umbo appears to be more pointed and elevated.

Range. This species is found from Beaufort, North Carolina south through the Greater and Lesser Antilles to Brasil.

Specimens examined. North Carolina: off Beaufort, in 6–9 fathoms; off Cape Hatteras, in 11–22 fathoms; off Cape Lookout, in 18–52 fathoms; off Cape Fear, in 14–18 fathoms (all USNM). Florida: St. Augustine; Lake Worth; Palm Beach; Triumph Reef; Long Reef; Ajax Reef; Key Largo; Turtle Harbor; Sambo Reef; Key West; Dry Tortugas (all USNM); Blind Pass and Tarpon Springs, Sanibel (both ANSP); Destin (MCZ). Mexico: off Cabo Catoche, Yucatan, in 640 fathoms (USNM). Bermuda: Castle Harbour; Harrington Sound (both MCZ). Bahama Islands: Bimini;

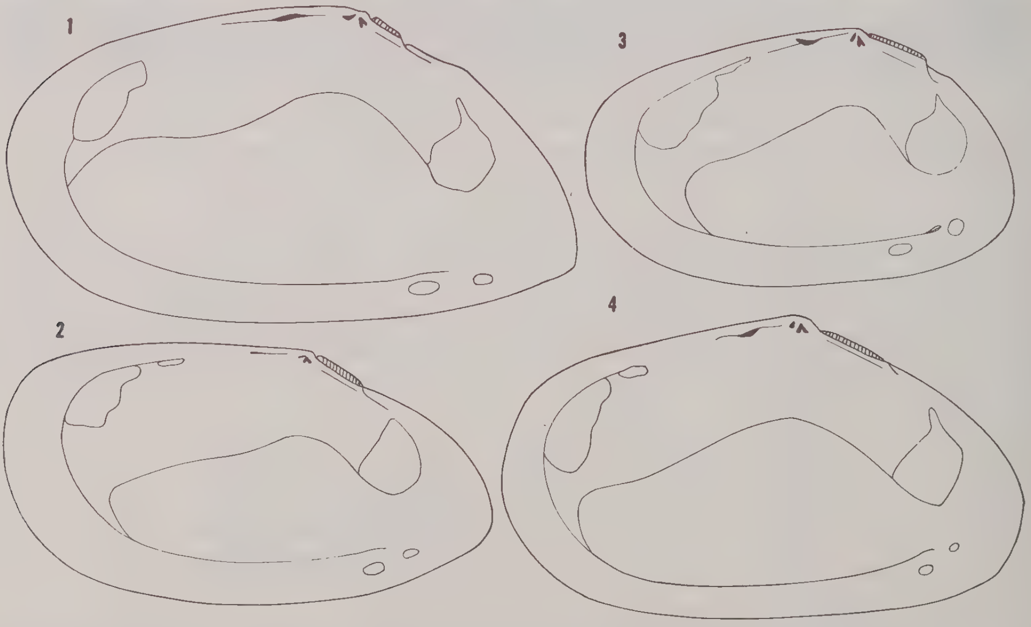

Plate 159. Figs. 1–4. Diagrammatic illustration of the internal surface of the right valve showing the dental configuration and muscle scars. Fig. 1. *Tellina versicolor* DeKay (about 6.8x) [L=12 mm.] Fig. 2. *Tellina euvitrea* Boss (about 3.4 x) [L=21 mm.]. Fig. 3. *Tellina probrina* Boss (about 3.5x) [L=18 mm.]. Fig. 4. *Tellina diantha* Boss (about 3.5x) [L=22 mm.].

New Providence; Andros (all USNM). Cuba: Cape Cajon; Punta Tolete; Santa Rosa; Bahia Honda; Cabanas (all USNM); Habana; Matanzas; Banes (all MCZ). Jamaica: (MCZ). Hispaniola. Haiti: Jeremie (USNM); Bizoton (MCZ). Puerto Rico: Mayagüez (IMBPR); La Parguera (MCZ); San Juan Harbor (USNM). Lesser Antilles: St. Lucia; Tobago (both MCZ). Caribbean Islands: Grand Cayman (ANSP). Brasil: off Natal; off Cape San Roque, in 20 fathoms; off Aracaju, Bahia in 12 fathoms (all MCZ).

Subgenus **Scissula** *Dall*

Scissula Dall 1900, Proc. U.S. Nat. Mus., **23**: 291 (type species, *Tellina decora* Say 1826 [= *Tellina similis* Sowerby 1806], original designation).

Cirsula Dall. Cary and Spaulding 1909, Bull. Gulf. Biol. Sta., **12**: 21, error for *Scissula*.

Description. Shell of small to medium size (up to $1\frac{1}{8}$ inches), and with or without a posterior flexure to the right. Sculpture consisting of weak, concentric lirations crossed by incised lines or scissulations which descend from the anterior slope or margin to the ventral margin. The posterior slope lacks the scissulate pattern of sculpture. Right anterior lateral tooth strong, laminate, and immediately proximal to the cardinal complex; all other laterals absent or obsolete. Pallial sinus rather extensive and deep but not coalescent with the anterior adductor muscle scar. Color of the shell white or red, suffused or rayed with white, red or yellow.

Scissula reaches its greatest development in the Eastern Pacific and, particularly, in the Western Atlantic regions. It is more or less tropical and subtropical in its distribution. In the Western Atlantic only a single species has a normal range which extends as far north as Cape Hatteras. In the Eastern Pacific, the northernmost limit for the subgenus appears to be the Gulf of California. In the Indo-Pacific, the group does not seem to have attained a similar level of development but such species as *Tellina micans* Hanley are decidedly scissulate and represent the subgenus in that realm. According to Woodring (1925), the earliest ancestors of the Western Atlantic species appeared in the Lower Miocene.

The precise definition of the subgenus delimits those species with scissulate sculpture on both valves. The content and status of *Scissula* has been contested by Salisbury (1934) who included the group with *Fabulina* Gray. The latter is uniquely typified by *Tellina fabula* Gmelin in which only the right valve is scissulate; this species is European and Mediterranean in its distribution. Since the structure of the right lateral dentition and the configuration of the pallial sinus in *Fabulina* and *Scissula* are very similar, a close relationship between the two groups cannot be denied. The approach of Thiele (1935) however will be employed in the present consideration, and *Scissula* and *Fabulina* will be treated as separate but closely allied subgenera.

Scissula is clearly related to the anguloid subgenera. The right valve possesses the diagnostic dental characteristics. The right anterior lateral tooth is typically long, thin, or shelf-like, more or less upturned, and closely adjacent to the cardinal complex. The right posterior lateral tooth is generally obsolete, except in *Tellina candeana*.

KEY TO THE SPECIES OF *SCISSULA* IN THE WESTERN ATLANTIC

1.	Shell subtrigonal and subsolid	*candeana*
	Shell elongate-elliptical	2
2.	Shell thin and fragile; generally with two posterior rays	3
	Shell thicker, not fragile, and often with numerous rays	4
3.	Shell white; scissulations broadly spaced (4–6 mm.)	*iris*
	Shell purple; scissulations closely spaced (6–10 mm.)	*sandix*
4.	Shell with strong concentric sculpture differentiated along the right posterior slope	*similis*
	Shell without distinctly differentiated concentric sculpture on the right posterior dorsal slope	*consobrina*

Tellina (Scissula) similis *Sowerby*

Plate 160, figs. 1–2

Tellina similis Sowerby 1806, British Miscellany, **2**: 29, pl. 75 (Brighton, England) [type locality, here restricted and corrected, Pelican Shoal, Florida; lectotype, here selected and figured, BMNH].

Tellina decora Say 1826, Jour. Acad. Nat. Sci., Philadelphia, **5**: 319 (southern coast of East Florida) [type locality, here restricted, South Inlet, Lake Worth, Florida; syntypes, ANSP 52427].

Tellina caribaea d'Orbigny 1842 [*in*] Sagra, Hist. L'Ile Cuba, Atlas, pl. 25, figs. 47–49; 1845, Spanish Text, **2**(5): 303 (Cuba y la Guadalupe); 1853, French Text, Mollusques, **2**: 251 [type locality, here restricted, Cuba; lectotype, here selected and figured, BMNH].

Tellina iris 'Say' Philippi 1845, Abbildungen und Beschreibungen, **2: Tellina**, p. 25, pl. 3, fig. 5.

Tellina eupareia Ravenel 1885, Proc. Elliot Soc., **2**(5): 37 (Sullivan's Island, South Carolina) [type lost].

Tellina (*Scissula*) *similis* Sowerby. Dall 1900, Proc. U.S. Nat. Mus., **23**: 296.

Description. Shell extending to 27.5 mm. (about $1\frac{1}{8}$ inches) in length and to 18.5 mm. (about $\frac{3}{4}$ inch) in height, elongate, subsolid to fragile, with the left valve more convex and with a strong posterior flexure to the right. Umbos posterior to the middle, opisthogyrous and blunt. Anterior margin smoothly and narrowly rounded; ventral margin convex and rising slightly posteriorly; anterior dorsal margin long, gently sloping and convex; posterior margin long and forming an oblique truncation. Sculpture consisting of weak concentric lirations which are strong on the right posterior slope and of acentric scissulations (about 7–9 per millimeter). Ligament light brown, short, broad, and protuberant. Calcareous portion of the ligament well developed and subtended by nymphal callosities. In the left valve, the cardinal complex consists of an anterior narrow, elongate, and strongly sulcated bifid tooth with equal lobes and of a thin, but strong laminate tooth; no true lateral teeth present. In the right valve, the cardinal complex consists of a posterior skewed bifid tooth whose posterior lobe is the larger and of an anterior thickened laminate tooth; anterior lateral tooth proximal to the cardinal complex, strong, and flangelike; posterior lateral tooth absent. Adductor muscle scars well impressed. Anterior adductor slightly larger and higher than the posterior adductor. Pallial sinus equal in both valves, rising slightly behind, convex above, and extending very near to but not coalescing with the anterior adductor. Externally the shell is predominantly white, sometimes suffused with yellow, red, or apricot; there are bands and rays of pink or red. Internally, the shell is shining and sometimes highly polished with the general color characteristics of the external surface.

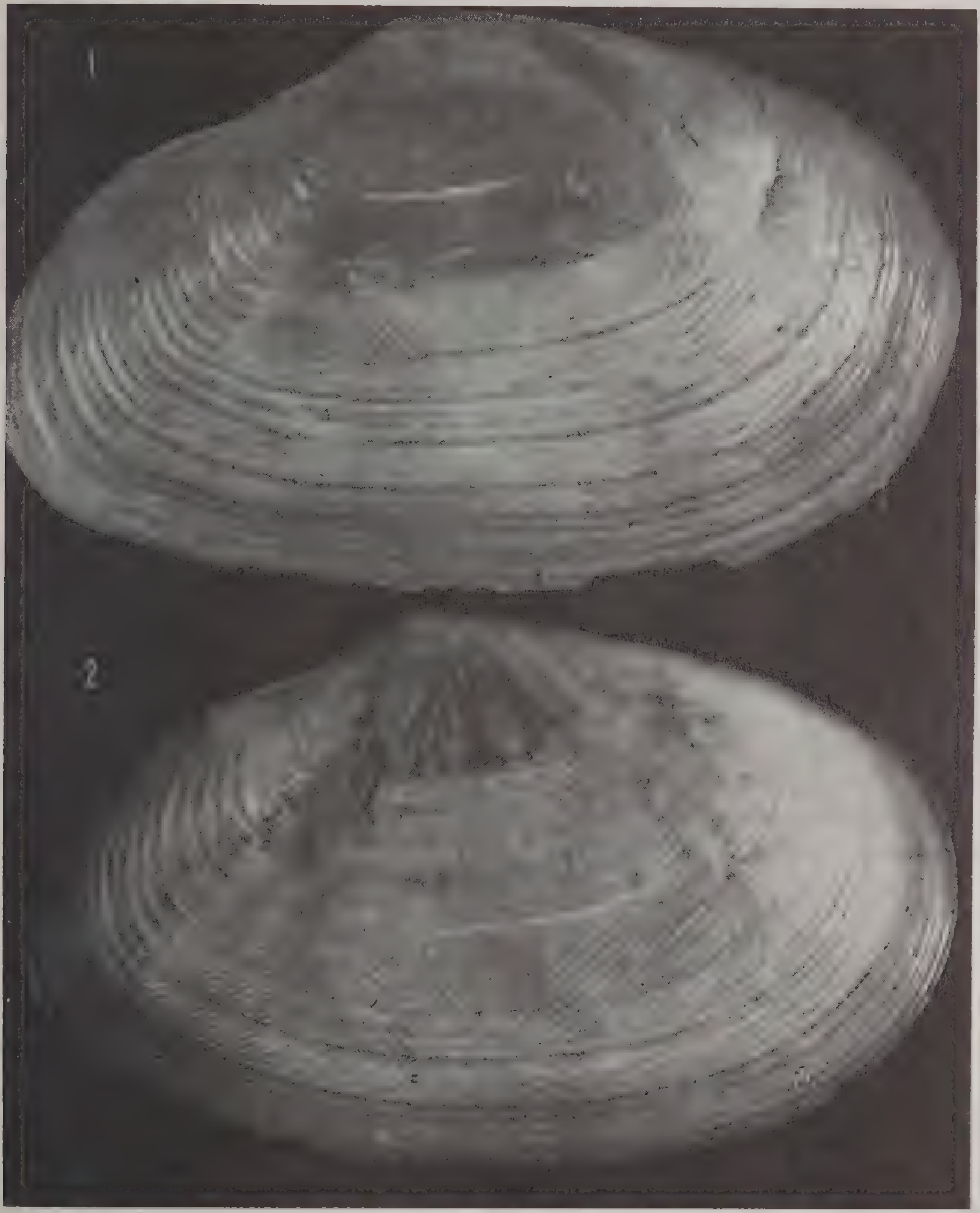

Plate 160. Fig. 1. *Tellina similis* Sowerby, external view of the right valve of the lectotype, Brighton, England, BMNH (about 9x) [L=17.5 mm.]. Fig. 2. *Tellina caribaea* d'Orbigny [=*Tellina similis* Sowerby], external view of the right valve of the lectotype, Cuba, BMNH (about 9x) [L=16.6 mm.].

length	height	width	
17.5 mm.	10.5 mm.	—	lectotype of *similis* Sowerby
16.6	9.7	4.3	lectotype of *caribaea* d'Orbigny
27.5	18.5	9.0	Tarpon Bay, Sanibel, Florida
18.0	11.5	6.0	Missouri Key, Florida
13.5	8.5	4.0	Cayo Caiman, Caibarien, Cuba
11.0	7.0	3.0	Grassy Key, Florida

Remarks. Among other Western Atlantic tellinids, *similis* might well be confused with *Temnoconcha brasiliana* Dall, for there is a superficial similarity of shape in these two species. A careful examination of the hinge mechanism and the dental formula will always show *similis* to be laterally dentate and *brasiliana* laterally edentate.

Tellina consobrina appears to be most closely related to *T. similis.* In the lack of differentiated posterior slope sculpture and in the obsolete condition of the scissulate sculpture, *consobrina* departs markedly from *similis. Tellina candeana*, because of the thickness of its valves and the disposition and spacing of the scissulations, may also be considered a close relative of *similis.* The two differ greatly in shape, *similis* being subquadrate, and *candeana* being subtrigonal, and the latter possesses a rather distinct right posterior lateral tooth. There is no analog of *similis* in the Eastern Pacific.

The fossil history of *Tellina similis* begins in the Oligocene [Miocene] of the Chipola horizon at Alum Bluff where Dall (1900b) has described *Tellina lampra*, which differs from the modern *similis* in being more inequilateral and, according to Dall, being differently shaped posteriorly. True *T. similis* appears in the Pliocene of the Caloosahatchie River, Florida, and it has been recorded in Pleistocene deposits on Grand Cayman Island in the Caribbean by Rehder (1962).

The depth range of this species includes shallow shore as well as off-shore records up to 130 fathoms. Bottom type preference seems to be limited to sand, particularly coarse sand.

Range. This species occurs normally from along the east coast of Florida in the vicinity of Lake Worth, south through the Antilles to Barbados and west as far as Panama; it has not been recorded in Trinidad nor along the coast of eastern South America.

Specimens examined. SOUTH CAROLINA: Isle of Palms (CM). FLORIDA: South Inlet, Lake Worth (ANSP); off Palm Beach), in 10–130 fathoms (MCZ); off Miami, in 10–24 fathoms; Bird Key, Biscayne Bay; off Fowey Light, in 6–40 fathoms; Hawk Channel, in 3-4 fathoms; Elliott Key (all USNM); Sand Key (MCZ); Ajax Reef, in 4 fathoms; Caesar's Creek Bank, in 10 feet; off Turtle Harbor, in 20 fathoms (all USNM); off The Elbow, Key Largo, in 21 fathoms (MCZ); Lower Matecumbe Key; Long Key (both USNM); Little Duck Key (D. and N. Schmidt); Grassy Key; Bonefish Key; Marathon, Key Vaca (all ANSP); SE of Looe Key, in 25-50 fathoms (MCZ); Sugar Loaf Key (ANSP); Pelican Shoal; Tea Table Key; Missouri Key (all MCZ); off Key West, in 5–10 fathoms; Dry Tortugas (both USNM); Naples (ANSP); Tarpon Bay, Sanibel; Boca Grande Key; Longboat Key; Gulfport (all MCZ); Anclote (USNM). MEXICO: Progreso; off Isla Mujeres (both MCZ). PANAMA: Colon (USNM). BAHAMA ISLANDS: Holmes Cay; Angel Fish Point, Little Abaco (both MCZ); Pensacola Cays, in 3 fathoms; Cat Cay, in 3 fathoms (both USNM); Whale Cay Channel; Dick's Point, Nassau, New Providence; Savannah Sound, Eleuthera; Little San Salvador; Russell Creek, Cat Island; Simms, Long Island; Matthew Town, Great Inagua (all

MCZ). Cuba: Cape Cajon; Punta Colorado, in 2–3 feet; Bahia Hondo, in 1–12 feet; Santa Rosa, in 3–6 feet; Esperanza, in 4–6 feet; Habana; Cabanas Harbor, in 3–12 fathoms; Cardenas, in 1–3 fathoms (all USNM); Cayo Caiman, Cayo Frances, Cayo Salina and Cayo Lucus, Caibarien (all MCZ); Punta Alegre, Camaguey; Cayo Largo, Oriente (both ANSP). Jamaica: (BMNH). Hispaniola. Santo Domingo: Samana (USNM). Puerto Rico: Cabo Rojo Light House (IMBPR). Virgin Islands: SE of East Point, in 6–20 feet, Anegada; West End Point, in 2–6 feet, Anegada; St. Thomas (all ANSP). Lesser Antilles: Guadeloupe (MCZ); St. Vincent (BMNH); off Paynes's Bay Church and off Telegraph Street, Barbados (both USNM). Caribbean Islands: E end of Frank South and Georgetown, Grand Cayman (both ANSP).

Tellina (Scissula) consobrina *d'Orbigny*

Plate 161, fig. 3; Plate 162, fig. 1

Tellina consobrina d'Orbigny 1842 [*in*] Sagra, Hist. L'Ile Cuba, Atlas, pl. 26, figs. 9–11; 1845, Spanish Text, **2**(5); 305 (en la arena de la Martinica); 1853, French Text, Mollusques, **2**: 254 [syntypes, BMNH 54.10.4.514].

Tellina (*Angulus*) *consobrina* d'Orbigny. McLean 1951, New York Acad. Sci., **17**(1): 96, p. 19, fig. 8.

Description. Shell extending to 14 mm. (about 9/16 inch) in length and to 8 mm. (about 5/16 inch) in height, elongate, fragile to subsolid, rather tumid with the left valve of a greater convexity and with a posterior flexure to the right. Umbos posterior to the middle, not elevated, small and blunt. Anterior margin smoothly and narrowly rounded; ventral margin straight to gently convex; anterior dorsal margin elongate, gently sloping, and slightly convex; posterior dorsal margin short and concave; posterior margin straight and forming an oblique truncation. Sculpture consisting of narrowly spaced, weakly developed and somewhat irregular concentric lines crossed by acentric scissulations (about 3–5 per millimeter) which are often obscure. Ligament light brown in color and protuberant. Calcareous portion of the ligament subtended by flattened and thickened nymphal callosities. In the left valve, the cardinal complex consists of a narrow anterior bifid tooth with equal lobes and of a posterior, thin, elongate laminate tooth often adpressed to the calcareous element of the ligament; no true lateral teeth present. In the right valve, the cardinal complex consists of a posterior, strongly skewed bifid tooth whose posterior lobe is much the larger and of an anterior thin to subdeltoid laminate tooth; the proximal anterior lateral tooth of varying thickness, projecting and often slightly upcurled; no posterior lateral tooth. Adductor muscle scars usually well impressed. Anterior adductor irregularly shaped, but elongate and rounded below; posterior adductor rounded. Pallial sinus more or less equal in opposite valves, rising abruptly and descending gently, and rounded in front. The shell is white, variously colored with red or pink rays, rarely completely white, or with anterior suffusions of pink. The external surface is smooth and shining and generally not iridescent.

length	height	width	
14.2 mm.	7.9 mm.	3.8 mm.	off Fowey Light, Florida
13.5	7.7	3.3	Key West Channel, Florida
10.8	6.1	—	Key Largo, Florida
9.3	5.5	2.0	Barbados, Lesser Antilles
8.3	4.8	1.9	St. Thomas, Virgin Islands

Remarks. Early authors considered *Tellina consobrina* to be a variety or southern form of *Tellina versicolor* DeKay. Although the latter encompasses a great range of variation, it may be segregated from *consobrina* by its pallial sinus which is closely adjacent to the anterior adductor muscle scar, its lack of scissulate sculpture and its more highly polished anterior surface. The internal surface of the valves of *consobrina* often tends to be thickened, irregular and not highly polished. In the present consideration, *versicolor* and *consobrina* are much more distantly related than previously assumed.

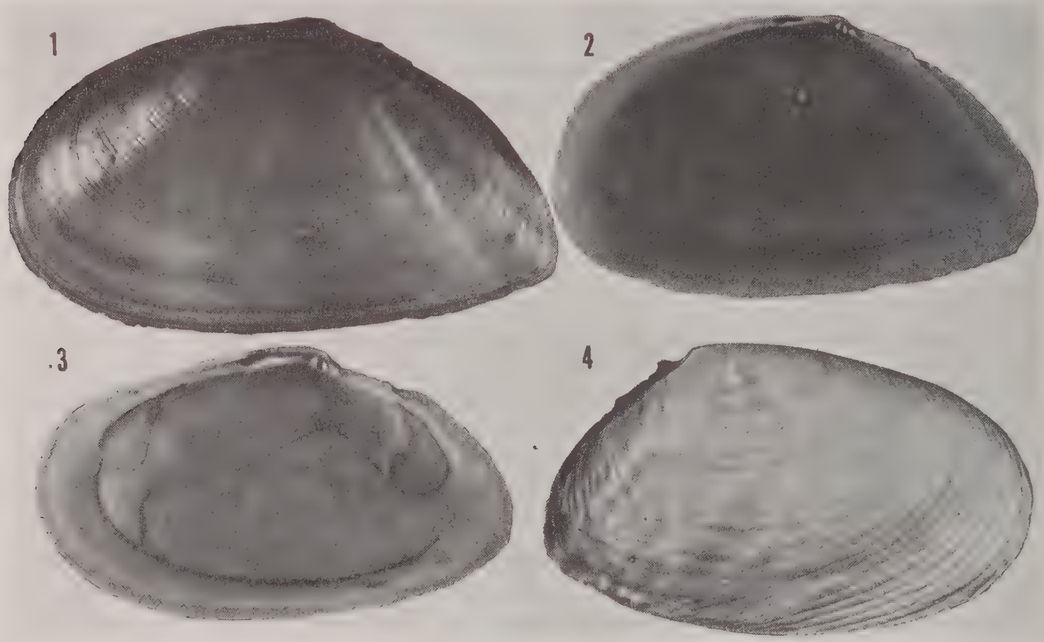

Plate 161. Figs. 1–2. *Tellina sandix* Boss. Fig. 1. External view of the left valve (about 4.7x) [L=17 mm.]. Fig. 2. Internal view of the right valve, Santa Barbara de Samana, MCZ 236333 (about 5.5x) [L=13 mm.]. Fig. 3. *Tellina consobrina* d'Orbigny, internal view of the right valve, off Fowey Light, Florida, USNM 462116 (about 5x) [L=14 mm.]. Fig. 4. *Tellina iris* Say, external view of the right valve, Fort Myers Beach, Florida, MCZ 243052 (about 7x) [L=10 mm.].

Tellina consobrina appears to be most closely related to *Tellina similis.* The acentric scissulate pattern of sculpture in *consobrina* is relatively obscure or obsolete when compared with the more closely set, well developed scissulations found in *similis.* No heavy and strongly developed concentric sculpture on the posterior slope of the right valve is differentiated in *consobrina,* whereas in *similis,* the presence of strong concentric sculpture in that area is diagnostic. In addition, the two species may be separated by the pallial sinus which in *consobrina* is higher and more distantly removed from the anterior adductor muscle scar.

Among the other species with which *Tellina consobrina* may be confused is *T. probrina.* The characters used to differentiate these two species have been discussed elsewhere (see *Remarks* under *T. probrina*).

Range. This species occurs from Miami, Florida through the Greater and Lesser Antilles to Tobago; it has also been discovered in Bermuda.

Specimens examined. FLORIDA: off Miami, in 24 fathoms; off Fowey Light, in 38–70 fathoms; Turtle Harbor; Key Largo; Key Vaca; Looe Key; Sambo Reef; Key West Channel; Dry Tortugas (all USNM). BERMUDA: Castle Rock (MCZ). CUBA: Cayo Arenas; Santa Lucia; Santa Rosa; Bahia Honda; Cabanas; Bahia de Cochinos (all USNM). PUERTO RICO: Mayagüez; La Parguera (both IMBPR); off Cape San Juan Light, in 26 fathoms (USNM). VIRGIN ISLANDS: St. Thomas (USNM). LESSER ANTILLES: Martinique (BMNH); English Harbour and Falmouth Harbour, Antigua; Barbados (all USNM); 2 miles S of Fort George, Scarborough, Tobago, in 36 fathoms (MCZ).

Tellina (Scissula) iris *Say*

Plate 161, fig. 4

Tellina iris Say 1822, Jour. Acad. Nat. Sci., Philadelphia, **2**: 302 (inhabits the southern shores) [type locality, here restricted, Sullivan's Island, South Carolina; holotype, ANSP 52375].

Tellina (*Angulus*) *iris* Say. H. and A. Adams 1856, Genera Recent Mollusca, **2**: 397.

Tellina plagia Ravenel 1885, Proc. Elliot Soc., **2**(5); 40 (on the beach near Charleston, South Carolina) [types lost].

Tellina (*Scissula*) *iris* Say. Dall 1900, Proc. U.S. Nat. Mus., **23**: 291.

Tellina (*Scissula*) *caribaea* 'd'Orbigny' Dall 1900, Proc. U.S. Nat. Mus., **23**: 297, *non* d'Orbigny 1842.

Tellina (*Cirsula*) *irrus* Say. Cary and Spaulding 1909, Bull. Gulf Biol. Sta., **12**: 21, errors for *Scissula* and *iris*.

Description. Shell extending to 15.3 mm. (about $\frac{5}{8}$ inch) in length and to 9 mm. (about $\frac{3}{8}$ inch) in height, elongate, elliptical, thin, rather compressed with both valves of equal convexity and with or without a very weak flexure to the right. Umbos posterior to the middle, small and somewhat pointed. Anterior margin smooth and rather narrowly rounded; ventral margin long, more or less straight, and rising slightly posteriorly; anterior dorsal margin long, gently sloping and slightly convex; posterior dorsal margin long, straight to slightly convex, and forming a broad slightly oblique truncation. Sculpture consisting of closely set, poorly developed, concentric incremental lines which are most noticeable on the posterior slope. The concentric sculpture is intersected and crossed by well developed, widely spaced scissulations which descend across the shell at an angle of 20–30 degrees (about 4–6 per millimeter). No radial sculpture. Ligament light yellow brown, short, generally weak and slightly protuberant. Calcareous portion of the ligament subtended by flange-like, elevated nymphal callosities. In the left valve, the cardinal complex consists of an anterior, small, narrowly elongate and protuberant bifid tooth with subequal lobes and of a posterior thin, elongate laminate tooth; no true lateral teeth present. In the right valve, the cardinal complex consists of a posterior strongly skewed bifid tooth whose posterior lobe is the larger and of an anterior thickened laminate tooth; anterior lateral tooth proximal to the cardinal complex, thin and laminate; posterior lateral tooth absent or obsolete, consisting of a distal thickening of the hinge plate. Adductor muscle scars rather poorly impressed. Anterior adductor irregularly quadrate; posterior adductor somewhat rounded. Pallial sinus rises abruptly posteriorly, descends gently and unites in an arcuation with the pallial line below; confluence extensive. The pallial sinus is separated by about one millimeter from the anterior adductor. Shell transparent to translucent, often extremely fragile, predominantly white or clear, but with some suffusion of red or pink. Two prominent white rays often occur in the posterior quarter of the disc. Internally the shell is smooth and polished.

length	height	width	
15.3 mm.	9.0 mm.	—	South Carolina
13.0	6.3	2.5 mm.	Galveston, Texas
12.5	7.0	2.5	Sea Island, Georgia
9.0	5.8	2.0	St. Petersburg, Florida

Remarks. This species possesses a small iridescent shell not unlike that of *T. versicolor*, and it has probably been confused with the latter a number of times since the two species are sympatric over most of their ranges. However, *versicolor* is distinctly separated from *iris* in the lack of scissulations. *Tellina iris* has scissulations, but often these sulci are obscured or in part destroyed or worn away, especially in the region of the central disc; therefore, one must be extremely careful in examining specimens to insure a proper identification. Scissulations even on old and worn specimens may generally be discerned along the ventral margin or on the extreme anterior slope. In addition, the pallial sinus of *iris* is removed from the anterior adductor muscle scar whereas that of *versicolor* is closely adjacent to that scar.

In the Western Atlantic, *iris* is most closely related to *T. sandix* which has a more southerly range. The former is a smaller species with a much shorter posterior dorsal slope and without the total pink or red coloration of *sandix;* the sculpture of *iris* is also noticeably more widely spaced. In the Eastern Pacific, *Tellina virgo* represents the nearest relative to *iris* though *iris* has a smaller shell with more widely spaced sulci and a differently angled posterior ridge.

In the fossil record of the Western Atlantic, Dall (1900b) described *Tellina scitula* (*non* Meek and Hayden, 1827) which has been renamed *healyi* by Woodring (1925). Dall indicated that this species occurs in the Miocene of Santo Domingo and of Bowden, Jamaica. Maury (1917) found it in the formations at Cercado de Mao and Rio Cana which illustrate its range through the Lower Miocene. In contrast to *iris*, *healyi* has finer, more oblique sulci and its posterior end is more pointed. Woodring (1925) in his discussion on *healyi* noted the resemblance of this species to certain *Eurytellina* and also mentioned that specimens of *healyi* from Santo Domingo, when compared to Bowden specimens possessed a thinner shell and a more slender nymph.

Range. This species extends as far north as North Carolina, in the vicinity of Cape Hatteras, south through the lower Florida Keys and west along the Gulf coast to Galveston, Texas. The greatest recorded depth is 17 fathoms and the species seems to prefer the inshore shallow areas along beaches.

Specimens examined. NORTH CAROLINA: Cape Hatteras Point; off Cape Hatteras, in 14–17 fathoms (both USNM). SOUTH CAROLINA: Sullivan's Island; Charleston; Folly Beach (all CM). GEORGIA: Sea Island (MCZ); Cumberland Island (CM). FLORIDA: Mayport; St. Augustine; Daytona Beach (all MCZ); off Miami, in 3 fathoms; Bahia Honda Key; Dry Tortugas; Caximba Pass; Marco Island; Bunch Beach; Punta Rassa (all D. and N. Schmidt); Sanibel; Bradenton Beach; St. Petersburg (all MCZ). LOUISIANA: Cameron (USNM). TEXAS: Sabine (MCZ); Galveston (ANSP).

Tellina (Scissula) sandix, new name
Plate 161, figs. 1–2

Tellina exilis Lamarck 1818, Animaux s. Vertebres, **5**: 527 (no locality given) [type locality, here restricted, Port Antonio, Jamaica; syntypes, Museum d'Histoire Naturelle, Geneva], *non* Meuschen 1787, *nec* Link 1808.

Tellina (*Angulus*) *exilis* Lamarck. H. and A. Adams 1856, Genera Recent Mollusca, **2**: 397.

Tellina (*Scissula*) *exilis* Lamarck. Dall 1900, Proc. U.S. Nat. Mus., **23**: 297.

Description. Shell extending to 19 mm. (about $\frac{3}{4}$ inch) in length and to 11 mm. (about $\frac{1}{2}$ inch) in height, elongate-subtrigonal, thin, fragile, compressed with both valves of equal convexity and with or without a very slight flexure to the right. Umbos posterior to middle, inconspicuous and rather blunt. Anterior margin smoothly and somewhat narrowly rounded; ventral margin nearly straight and rising only slightly posteriorly; anterior dorsal margin long, gently sloping, and convex; posterior dorsal margin long and rather steeply sloping; posterior margin short, ill defined, generally straight, and forming a small posterior truncation. Sculpture consisting of poorly defined, closely set concentric incremental bands which are intersected by closely set and finely incised scissulations (about 10 per millimeter) which cross at an angle of 30 degrees. No radial sculpture present. Ligament brown, rather short, weak and not protuberant. Calcareous portion of the ligament subtended by short, but slightly raised nymphal callosities. In the left valve, the cardinal complex consists of an anterior narrow, elongate, deeply cleft bifid tooth with equal lobes and of a posterior divergent, extremely long and thin laminate tooth; no true lateral dentition present. In the right valve, the cardinal complex consists of a posterior, strongly skewed, well developed bifid tooth whose posterior lobe is much the larger and of an anterior, variously developed laminate tooth; anterior lateral tooth proximal to the cardinal complex, long, thin and laminate; posterior lateral tooth absent or obsolete, consisting of a distal thickening of the hinge plate. Adductor muscle scars moderately well impressed. Anterior adductor irregularly elongate; posterior adductor round. Pallial sinus rising rather abruptly posteriorly, extending almost to, but not confluent with the anterior adductor, descending gently and arcuately falling to the pallial line; confluence complete. Shell transparent, translucent, predominately crimson suffused with pink or white, often with white rays posteriorly. Rarely iridescent. The internal surface is shining, but not highly polished.

length	height	width	
15.6 mm.	9.2 mm.	3.2 mm.	Syntype of *exilis* Lamarck
19.0	11.0	—	Monte Cristi, Santo Domingo
17.2	10.2	3.3	Guadeloupe
14.5	10.5	—	"
12.0	8.0	—	Jamaica

Remarks. This species has often been confused with the more northerly *Tellina iris* Say to which it is very closely allied. The scissulations of *sandix* number about 10 per millimeter whereas in *iris* they are more widely spaced, numbering about 4–6 per millimeter. The angle of descent of the sulci across the surface of the valves is nearly the same in both species. In color, *sandix* is nearly always pink or red with some indication of colored rays posteriorly while *iris* is usually white and its posterior rays may be poorly or well developed. The descent of the posterior dorsal slope is especially diagnostic in *sandix* and serves to differentiate *iris* as well. In *sandix*, this slope is characteristically elongate and somewhat steeply inclined, giving the posterior portion a produced appearance whereas the posterior slope in *iris* is markedly shorter and more steeply inclined. The pallial sinus of *iris* is typically further removed from the anterior adductor muscle scar than it is in *sandix.*

Among the variations exhibited by *Tellina sandix,* none seems as important as the thickness of the valves; some specimens are heavier than others, being opaque rather than completely translucent or even at times transparent. The extreme thinness of the valves makes them relatively fragile.

According to Dall (1900a), *Tellina sandix* is related to the Eastern Pacific species, *Tellina virgo* Hanley, and they may be separated in that the former is more compressed, more arcuate and less pointed behind. However, *T. esmeralda* Olsson seems even more closely allied to *sandix* than *virgo,* and the latter may, in turn, be considered closely related to *iris* (see *Remarks* under *iris*). In the Tertiary of the Western Atlantic, there does not seem to be any obvious precursor to *sandix.*

Range. This species appears to possess a distribution that is distinctly Antillean and South American. Although Aguayo and Jaume list this species in their catalog of the mollusks of Cuba, the northernmost record which is preserved in the museums in this country is from Jamaica. Excluding Cuba, the range of this species extends from the Greater Antilles, through the Lesser Antilles, and along the South American coast to Uruguay.

Specimens examined. JAMAICA: Port Antonio; Port Morant (both MCZ). HISPANIOLA. HAITI: Baie Anglaise; Aquin (both USNM). SANTO DOMINGO: Monte Cristi; Santa Barbara de Samana (both MCZ). PUERTO RICO: Isla Desecheo; Punta Guanajibo (both IMBPR). LESSER ANTILLES: Guadeloupe (ANSP; MCZ). BRASIL: Thayer Expedition (MCZ); Santos (USNM). URUGUAY: La Paloma Rocha (USNM)

Tellina (Scissula) candeana *d'Orbigny*

Plate 162, fig. 2

Tellina candeana d'Orbigny 1842 [*in*] Sagra, Hist. L'Ile Cuba, Atlas, pl. 25, figs. 50–52; 1845, Spanish Text, **2**(5): 303 (Martinica); 1853, French Text, Mollusques, **2**: 254 [lectotype, here selected and figured, BMNH 54.10.4.503].

Tellina (*Scissula*) *candeana* d'Orbigny. Dall 1900, Proc. U.S. Nat. Mus., **23**: 297.

Tellina (*Anbulus*) *candeana* d'Orbigny. McLean 1951, New York Acad. Sci., **17**(1): 97, pl. 20, fig. 2 (error for *Angulus*).

Description. Shell extending to 16 mm. (about $\frac{5}{8}$ inch) in length and to 10 mm. (about $\frac{3}{8}$ inch) in height, elongate-subtrigonal, inflated with the left valve of greater convexity and with a strong posterior flexure to the right. Umbos posterior to the middle, opisthogyrous and blunt. Anterior margin smoothly and narrowly rounded; ventral margin convex and rising gently in the posterior arcuation; anterior dorsal margin very long, gently sloping, more or less straight; posterior dorsal margin long, steeply sloping and straight; posterior margin rather ill defined, straight and forming an oblique truncation. Sculpture consisting of closely set, raised concentric lirations limited to the posterior slope; the disc of the shell and the anterior slope are covered with closely set scissulations (about 7–8 per millimeter) which descend obliquely across the surface of the shell at an angle of about 50 degrees. No radial sculpture present. Ligament light brown, short, rather weak and slightly protuberant. Nymphal plate without raised callosities. In the left valve, the cardinal complex consists of an anterior narrow and elongate bifid tooth with subequal lobes and of a posterior thin, laminate tooth; no true lateral teeth present. In the right valve, the cardinal complex consists of a posterior, slightly skewed bifid tooth whose posterior lobe is the larger and of an anterior, somewhat thickened laminate tooth; anterior lateral tooth strong, proximal to the cardinal complex, elongate and laminate; the posterior lateral tooth is distal to the cardinal complex, small, pointed and variously developed though never as strong as the anterior lateral. Adductor muscle scars fairly well impressed. The anterior adductor quadrate; the posterior adductor round. Pallial sinus equal in both valves, rising slightly posteriorly to a blunt apex, descending gently and falling arcuately to the pallial line; confluence extensive. The pallial sinus is separated from the anterior adductor by about 0.5 mm. The shell is smooth, shining, white, and often suffused with yellow or pink; the suffusion may be localized on the disc or include the entire valve. Internally, smooth and rather highly polished, white, or with yellow or pink suffusions.

length	height	width	
10.5 mm.	8.0 mm.	3.8 mm.	Lectotype of *candeana* d'Orb.
16.0	10.0	5.0	Turks Island, Bahamas
14.0	8.5	4.5	Grassy Key, Florida
12.0	8.1	3.5	Santa Rosa, Cuba
8.2	5.5	2.8	Grand Cayman Island

Remarks. This species, as evidenced by the measurements, possesses some variability with regard to shape, but in outline, the shell always appears to be subtrigonal. In color, *candeana* is predominantly white but occasionally specimens which are completely pink are encountered. The usual coloration in young individuals is white with umbonal suffusions of yellow or yellow-green. From the basic morphological pattern of *Scissula*, *candeana* is divergent, and there is some evidence, particularly in the strength of the right posterior lateral tooth, that may indicate that the species could be removed from the scissulate group. However, the thickness of the shell, the angle of the descent of the oblique sulci and the character of the pallial sinus present evidence that *candeana* is related to *similis*. Among other characters, these species may be separated most easily on

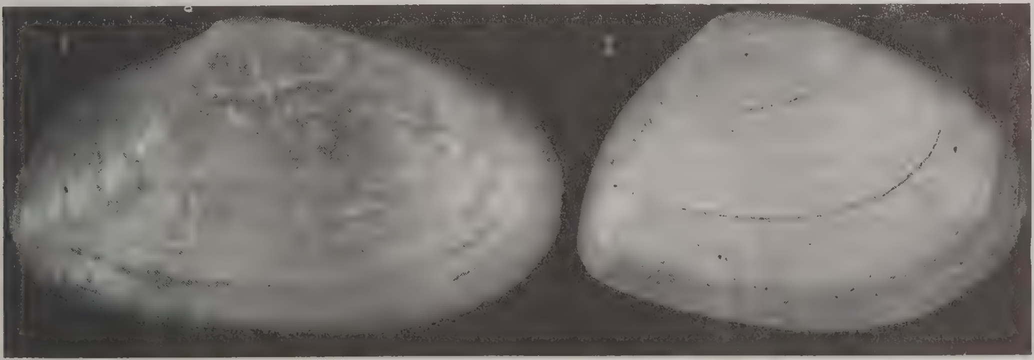

Plate 162. Fig. 1. *Tellina consobrina* d'Orbigny, external view of the right valve of the syntype, Martinique, BMNH (about 6.3x) [L=12.3 mm.]. Fig. 2. *Tellina candeana* d'Orbigny, external view of the right valve of the lectotype, Martinique, BMNH (about 6x) [L=10.5 mm.].

shape alone, where *similis* is subquadrate and *candeana* is subtrigonal. There are no species in the Eastern Pacific with which *candeana* could be closely related or confused. In the fossil record of the Western Atlantic, *Tellina calliglypta* Dall seems most closely allied to *candeana* and Olsson and Harbison (1953) have recorded the occurrence of the latter in the Pliocene of Florida. Rehder (1962) has listed *candeana* from the Pleistocene deposits on Grand Cayman Island.

Robertson (1959) has described the habitat of this species in the Bahamas. Usually, the species occurs among the rhizomes of *Thalassia*, but sometimes it may be found in sand substrates which are devoid of large plants. He also found large numbers of dead specimens of *candeana* in mud substrates at the northern end of North Sound, Bimini. The greatest depth recorded for this species is 6 fathoms, and Abbott (1958) has given its depth range at Grand Cayman as being between 6 and 25 feet.

Range. The northernmost continental extension of the range of this species is the southeastern coast of Florida, off Palm Beach; it is found in Bermuda, through the Bahamas, and south through the Lesser Antilles to Guadeloupe.

Specimens examined. FLORIDA: off Palm Beach (MCZ); off Miami; off Caesar's Creek Bank (both USNM); Grassy Key; Key Vaca (both D. and N. Schmidt); Newfound Harbor Key; Key West; Boca Grande Key; Cedar Key (all USNM). BERMUDA: Castle Island (USNM); Castle Rock; North Rock, in 4 fathoms (both MCZ). BAHAMA ISLANDS: Bimini (MCZ); Cat Cay; off Mintie Bar, Andros; New Providence (all USNM); Governor's Harbour and Savannah Sound, Eleuthera; Orange Creek and Camptown, Cat Island; Little San Salvador; Simms, Long Island; Turks Island (all MCZ). CUBA: Cayo Levisa; Santa Rosa (both USNM); La Sortija, Caibarien; Guarda la Vaca, Banes, Oriente (both MCZ). VIRGIN ISLANDS: Anegada; St. Thomas; St. Croix (all ANSP). LESSER ANTILLES: Martinique (BMNH); Guadeloupe (MCZ). CARIBBEAN ISLANDS: Gun Bay, West Beach, and Frank Sound, Grand Cayman (all ANSP).

Genus **Tellidora** *H. and A. Adams*

Tellidora (Mörch MS) H. and A. Adams 1856, Genera Recent Mollusca, **2**: 401 (type species, *Tellina burneti* Broderip and Sowerby 1829, subsequent designation Stoliczka, 1870, p. 116).

Tellipiura Olsson 1944, Bull. Amer. Paleo., Ithaca, N.Y., **28**: 221 (type species, *Tellidora* (*Tellipiura*) *peruana* Olsson 1944, original designation).

Description. Shell of medium size, trigonal, valves of unequal convexity, relatively thin, more or less equilateral, somewhat compressed; umbos high and centrally located; dorsal margin in distinct anterior and posterior portions both of which are spinose; two cardinal teeth in each valve, one bifid and one laminate; two lateral teeth in each valve, stronger in the right valve; surface of the valves more or less smooth but with growth lines and concentric sculpture. Ligament immersed and relatively short. Pallial sinus extensive, ascendant and nearly half of its lower margin confluent with the pallial line.

As has been noted by Dall (1900) and Olsson and Harbison (1953), the generic name *Tellidora* has often been attributed to Mörch, as indeed it had been by H. and A. Adams; however, there is no published usage of this name by Mörch prior to 1856. Two Recent species of this genus occur, one in the Western Atlantic region and another in the Eastern Pacific. Adams described two species, *pellyana* from the Persian Gulf and *pusilla* from the Red Sea which he assigned to *Tellidora* but both appear to belong to *Merisca* or another related group.

Tellidora cristata (*Recluz*)

Plate 163, figs. 1–2

Lucina cristata Recluz 1842, Revue Zool. Societé Cuvier., **5:** 270 (Campeche Banks); Guerin 1843, Mag. de Zool., pl. 60, 5 figs. [types not seen].

Tellidora (*Tellina*) *lunulata* H. and A. Adams 1856, Genera Recent Mollusca, **2:** 401 [types not seen].

Tellidora lunulata H. and A. Adams [*in*] Holmes 1860, Post-Pleiocene Fossils of South Carolina, p. 47, pl. 9, figs. 7–7d (St. Andrews, South Carolina).

Tellidora cristata Recluz. Dall 1889, Bull. No. 37, U.S. Nat. Mus., p. 62.

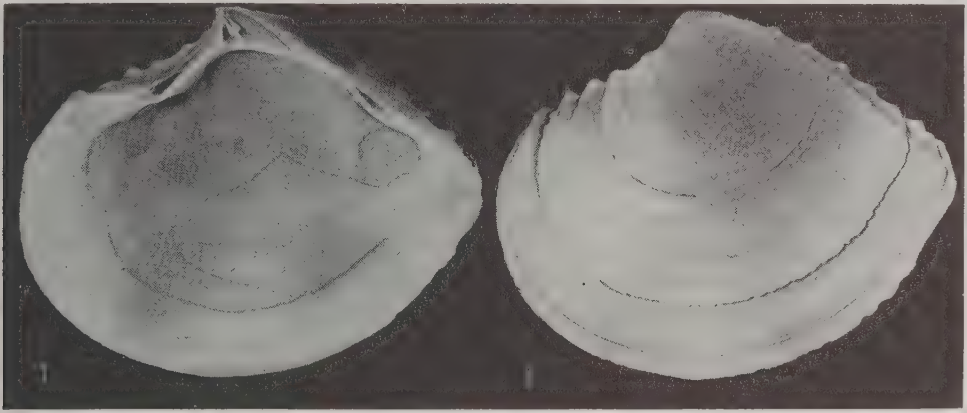

Plate 163. *Tellidora cristata* (Recluz). Fig. 1. Internal view of the right valve. Fig. 2. External view of the left valve, Progreso, Yucatan, MCZ 23589 (about 1.8x) [L=37 mm.].

Description. Shell reaching 37 mm. (about $1\frac{1}{2}$ inches) in length and 30 mm. (about $1\frac{1}{4}$ inches) in height, subtrigonal, subsolid, compressed, without or with only a slight posterior flexure to the right and with the valves thin to fragile in immature stages. The left valve is much flattened and the right valve is tumid and convex. Umbos central, acute and elevated. Anterior margin broadly rounded; ventral margin rounded, rising posteriorly in an arcuation; posterior margin straight, extremely short and forming a truncation. Anterior and posterior dorsal margins with triangular spinosities. Sculpture consisting of strong narrow ridges somewhat irregularly and broadly spaced and not raised in older specimens. Ligament light brown, short and partially internal. The spines of the dorsal margin form a deep lunule and escutcheon. In the left valve, the posterior single laminate cardinal tooth generally weak and tending to become obsolete; anterior cardinal tooth weakly bifid; both lateral teeth distal to the cardinal complex. In the right valve, the single anterior laminate cardinal tooth narrow and weak in young specimens, obsolete in adults; posterior bifid cardinal tooth long and narrow; posterior lateral tooth distal to the cardinal complex and well developed but weaker than the strong, subproximal anterior lateral tooth. Adductor muscle scars well impressed. Anterior and posterior adductor muscle scars subequal; posterior scar nearly rounded. Pallial sinus similar in both valves, short, widely separated from the anterior adductor scar, falling arcuately to the pallial line and uniting with it posteriorly. The shell and umbo are milk-white internally and externally.

length	height	width	
36.8 mm.	29.0 mm.	6.5 mm.	Progreso, Yucatan
29.0	22.9	5.5	Cortez, Florida
26.7	20.2	4.2	Sanibel Island, Florida
13.0	10.2	2.2	Little Marco Island, Florida

Remarks. This species is the only living member of the genus in the Western Atlantic, and as such is easily recognized. Its peculiar trigonal shape combined with the dorsal extensions of the concentric sculpture immediately separate it from other species. Its nearest relative and closest ally, *Tellidora burneti*, occurs in the Eastern Pacific. From this species *cristata* may be distinguished by its convex right valve, flattened left valve, lower proportions and less convex anterior dorsal margin. It is interesting to note that the convexity and concavity of the valves in *burneti* is directly opposite in *cristata;* in *burneti*, the right valve is much flattened and noticeably concave whereas the left valve is convex.

Tellidora cristata is represented in the fossil history of the Western Atlantic by what has been called *Tellidora lunulata* 'Holmes' H. and A. Adams. This Pliocene and Pleistocene fossil is considered to be a synonym of the Recent species following the treatment by Dall (1900a). It has been recorded in the Pliocene and Pleistocene strata of Florida, the Carolinas and the Gulf Coast States.

This species is a shallow water form and Parker (1960) has delineated it in the inlet and deep channel faunal assemblages in the northern Gulf of Mexico. It prefers a bottom type which is predominantly sandy, at depths ranging from 8 to 45 feet.

Range. This species is found from Beaufort, North Carolina to the Florida Keys and along the Gulf Coast to Yucatan, Mexico.

Specimens examined. NORTH CAROLINA: Beaufort (USNM). SOUTH CAROLINA: Isle of Palms (CM). FLORIDA: Fort George; Key Largo; Pine Key; Cape Romano (all USNM); Little Marco Island; Sanibel; Tarpon Bay; Charlotte Harbor; Lemon Bay; Siesta Key; Cortez; Gulfport; Sea Horse Key, Cedar Keys (all MCZ). ALABAMA: Fort Morgan (MCZ). LOUISIANA: Santa Rosa Sound (USNM). TEXAS: Pass Cabello (USNM); Port Aransas (MCZ). MEXICO: Campeche (ANSP); Progreso, Yucatan (MCZ).

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Age, Length, and Gonadal Stages of Herring from Georges Bank and the Gulf of Maine

BY H. C. BOYAR[1]

Abstract

Age, length, and gonadal stages of adult herring, *Clupea harengus harengus* L., were determined from samples collected in 1960–65 from Georges Bank and the Gulf of Maine. Age-groups IV and V were the most abundant ages in the samples. The 1960 year-class dominated the samples from Georges Bank in 1963–65, and the samples from the Gulf of Maine in 1964–65. This year-class was the most abundant during the period of study. The 1959 year-class was extremely weak on Georges Bank, but was well represented in the Gulf of Maine. The mean lengths of the age-groups IV and V from the 1960 year-class were generally less than those from other year-classes; the slow growth and the apparent high abundance suggest that growth is density-dependent. Differences in the peak of spawning and spawning seasons among the areas were small.

Introduction

Until 1961 the traditional harvest of herring, *Clupea harengus harengus* L., in the Gulf of Maine was largely from the inshore fishery for immature fish (sardines); the only significant fishery for adult herring was in southern Nova Scotia. In 1961, the USSR established a fishery for adult herring on Georges Bank (offshore Gulf of Maine); the annual catch from that fishery has exceeded the inshore catch for the State of Maine in every year through 1965. The average catches for these 5 years by the USSR and the State of Maine were about 108,000 and 47,000 metric tons, respectively. To date the development of the offshore fishery has given no evidence of any effect on the sardine fishery. It is not known whether the offshore spawning contributes to the inshore populations of sardines, or if the adult populations are discrete. One way to determine the relationship of offshore and inshore populations of herring is to compare the biological characteristics of fish from known spawning sites. The data compared in this report include information on age, length, and gonadal stages of herring from the Gulf of Maine and Georges Bank where the spawning has been documented (Moore, 1898; Huntsman, 1919; McNairn, 1933; Fish and Johnson, 1937; Sanders, 1952; Bigelow and Schroeder, 1953; Tibbo, 1957; Leim, 1958; Tibbo, Legare, Scattergood, and Temple, 1958; Colton and Temple, 1961).

Collection of Samples

Samples from the Gulf of Maine were divided into two groups — those from the United States coastal area between Cape Cod, Massachusetts, and Eastport, Maine, and those from the southern coast of Nova Scotia between St. Mary's Bay and Port Mouton (Fig. 1). The US areas are referred to collectively as the Coastal Gulf of Maine. Three sites provided the majority of the samples: Eastport and Boothbay Harbor, Maine, and Cape Cod, Massachusetts. Additional samples were taken from Isles of Shoals, Matinicus, and Monhegan Island. Herring from Isles of Shoals were available only during the spring and late autumn, and herring from Matinicus and Monhegan Islands were taken during the summer.

Samples from Nova Scotia were collected from Trinity Ledges eastward to Port Mouton in June–September. Samples of herring obtained during May, October, and December were from the St. Mary's Bay area on the western coast of Nova Scotia.

In April, Georges Bank herring occurred between the Southwest Part and Southeast Part of the Bank and west of Cultivator Shoals, but were absent from the Northern Part of the Bank. In June and July, herring were evenly dispersed throughout the Bank; approximately equal catches per unit of time were obtained from trawl drags on the Southwest Part, Southeast Part, Northeast Peak, Northern Edge, and the Northern Part as far west as Cultivator Shoals. Our findings of herring throughout the Bank during

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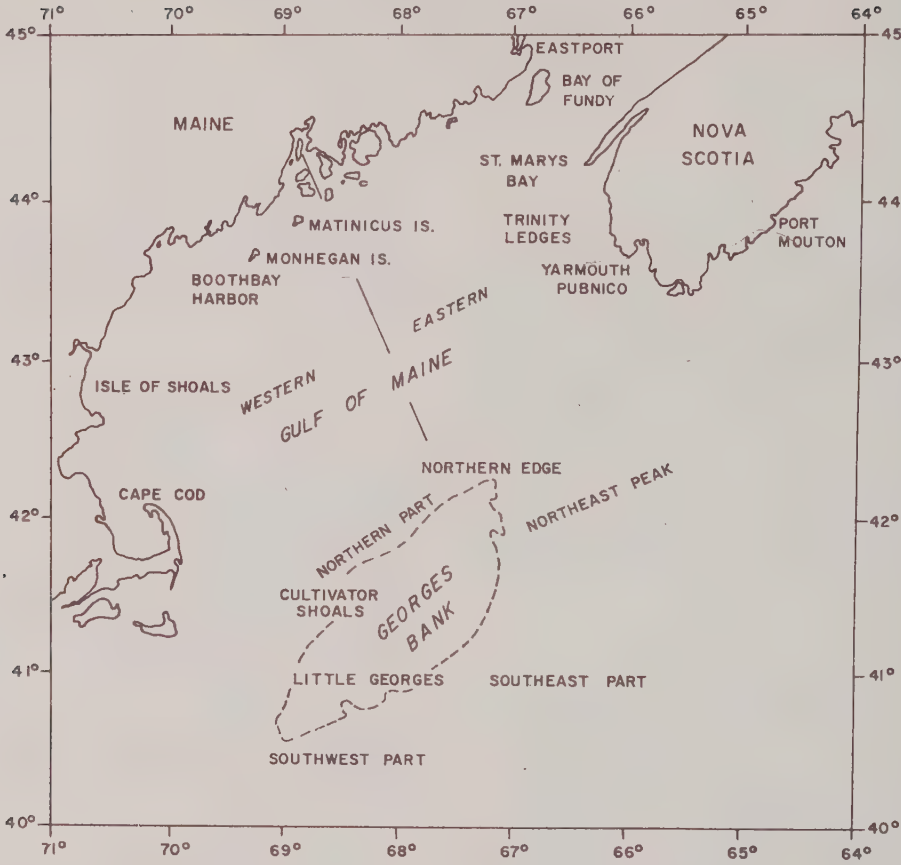
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BAY OF FUNDY
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NOVA SCOTIA
ST. MARYS BAY
MATINICUS IS.
TRINITY LEDGES
PORT MOUTON
MONHEGAN IS.
BOOTHBAY HARBOR
YARMOUTH
PUBNICO
EASTERN
WESTERN
GULF OF MAINE
ISLE OF SHOALS
NORTHERN EDGE
CAPE COD
NORTHERN PART
NORTHEAST PEAK
CULTIVATOR SHOALS
GEORGES BANK
LITTLE GEORGES
SOUTHEAST PART
SOUTHWEST PART

Fig. 1. Areas of sampling for herring on Georges Bank, coastal Gulf of Maine, and Nova Scotia.

TABLE 1. Length at age and percentage of age composition from samples of herring caught with gill nets, trawls, and purse seines from Georges Bank, Coastal Gulf of Maine, and Nova Scotia, June 1964. Number of fish in parentheses.

	Georges Bank				Coastal Gulf of Maine				Nova Scotia	
	Gill net (310)		Dutch trawl (762)		Purse seine (200)		Commercial trawl (52)		Gill net (529)	
Age-group	%	Average length	%	Average length	%	Average length	%	Average length	%	Average length
		cm		*cm*		*cm*		*cm*		*cm*
III	1	22.8	—	—	5	23.4	5	21.8	—	—
IV	66	26.5	63	26.7	89	25.9	76	26.0	29	25.9
V	8	29.0	7	29.3	4	29.4	11	28.9	9	28.5
VI	20	30.2	21	30.2	2	31.2	8	30.4	22	30.3
VII	5	31.4	9	30.8	—	—	—	—	27	31.4
VIII	—	—	—	—	—	—	—	—	8	32.2
VIII+	—	—	—	—	—	—	—	—	5	33.7

June 1964 and 1965 differed from those of Bryantsev (1966) who reported that herring did not move in a northerly direction beyond the Southeast Slope in June–July 1962. From August through November, herring congregated on the Northern Part of the Bank (west of Cultivator Shoals to the Northern Edge).

Trawls were the principal gear for the collection of herring on Georges Bank. In waters where trawling was not possible, we used gill nets. In the Coastal Gulf of Maine, the majority of the herring were obtained with trawls; occasional samples were collected from gill nets and purse seines. Most of the fish were taken in waters beyond the limit of the stop seines and weirs which are fished in the inshore fishery. Herring from Nova Scotia were obtained primarily by gill nets, but some came from weirs.

The lengths of fish of the various age-groups and the age compositions for herring caught with the different gears used in each area were compared to determine whether there was any bias because of selection of gear (Table 1). Although a detailed analysis of the selective action of the gear is beyond the scope of this report, a limited comparison of the tabulated data reveals no major bias. Herring (exclusive of the immature fish) caught with the various types of gear were similar in size for a particular age-group, and the same age-group (IV) dominated all the samples (weakly in Nova Scotia) regardless of the gear used.

The commercial fishermen used nylon gill nets with a mesh of $2\frac{3}{8}$- to 3-inch (61- to 76-mm) stretched measure and generally caught adult fish. Aboard research vessels, gill nets ranged from 1 to $2\frac{3}{4}$ inches (25 to 70 mm) stretched mesh and caught both immature and adult fish. Fishermen on commercial draggers caught herring with trawls that had a stretched mesh of 2 inches (51 mm) in the body, and 1-inch (25-mm) liner in the codend. Scientists aboard the research vessels caught herring with a Dutch herring trawl that was lined from belly to codend with a 1-inch (25-mm) stretched mesh. The trawls caught all sizes of herring. Samples from purse and stop seines, and weirs ($\frac{1}{4}$- to 1-inch stretched mesh — 6- to 25- mm) were not considered selective either and contained fish of all age groups present on the grounds. Fish of age-group II have been included in the Georges Bank data because they were taken in sufficient abundance to help describe that population. To obtain an index of population structure of the adult herring in Coastal Gulf of Maine, age-groups III and upward were used; very few fish of age-groups I and II (less than 150 fish) were taken. No fish of the age-groups I and II were obtained from Nova Scotia, and no fish of age-group I from Georges Bank.

In 1960–65, 112 samples (9,880 herring) from Georges Bank, 160 samples (11,435 herring) from Coastal Gulf of Maine, and 81 samples (7,436 herring) from Nova Scotia were obtained for study (Table 2). Whenever possible, monthly samples of at least 100 fish were collected.

TABLE 2. Number of samples and total number of herring collected in different years from Georges Bank, Coastal Gulf of Maine, and Nova Scotia, 1960–65.

	Georges Bank		Coastal Gulf of Maine		Nova Scotia	
	Number of		Number of		Number of	
Year	Samples	Fish	Samples	Fish	Samples	Fish
1960	5	571	1	106	5	384
1961	3	588	6	282	4	490
1962	13	1,080	1	251	7	850
1963	24	3,044	35	2,398	20	1,797
1964	35	2,549	46	3,565	20	1,787
1965	32	2,048	71	4,833	25	2,128
Total	112	9,880	160	11,435	81	7,436

Age and Length

Age determinations were made from otoliths. The age was recorded as the number of actual or virtual summer growth zones on the otolith. The year-class to which a fish belonged was also recorded and refers to the year of deposition and hatching of the majority of the eggs. It was assumed that all fish spawned in the autumn were hatched before 1 January; for fish spawned in the spring, hatching took place between April and June. Virtually all of the spawning, however, occurred in the fall. In accordance with International Commission for the Northwest Atlantic Fisheries (ICNAF) procedures, all fish older than age-group VIII were combined into a VIII+ category. Since the I and II group fish were eliminated from the Coastal Gulf of Maine and Nova Scotia samples, the age scale is from II to VIII+ for herring of Georges Bank, and III to VIII+ for herring from Coastal Gulf of Maine and Nova Scotia (Fig. 2).

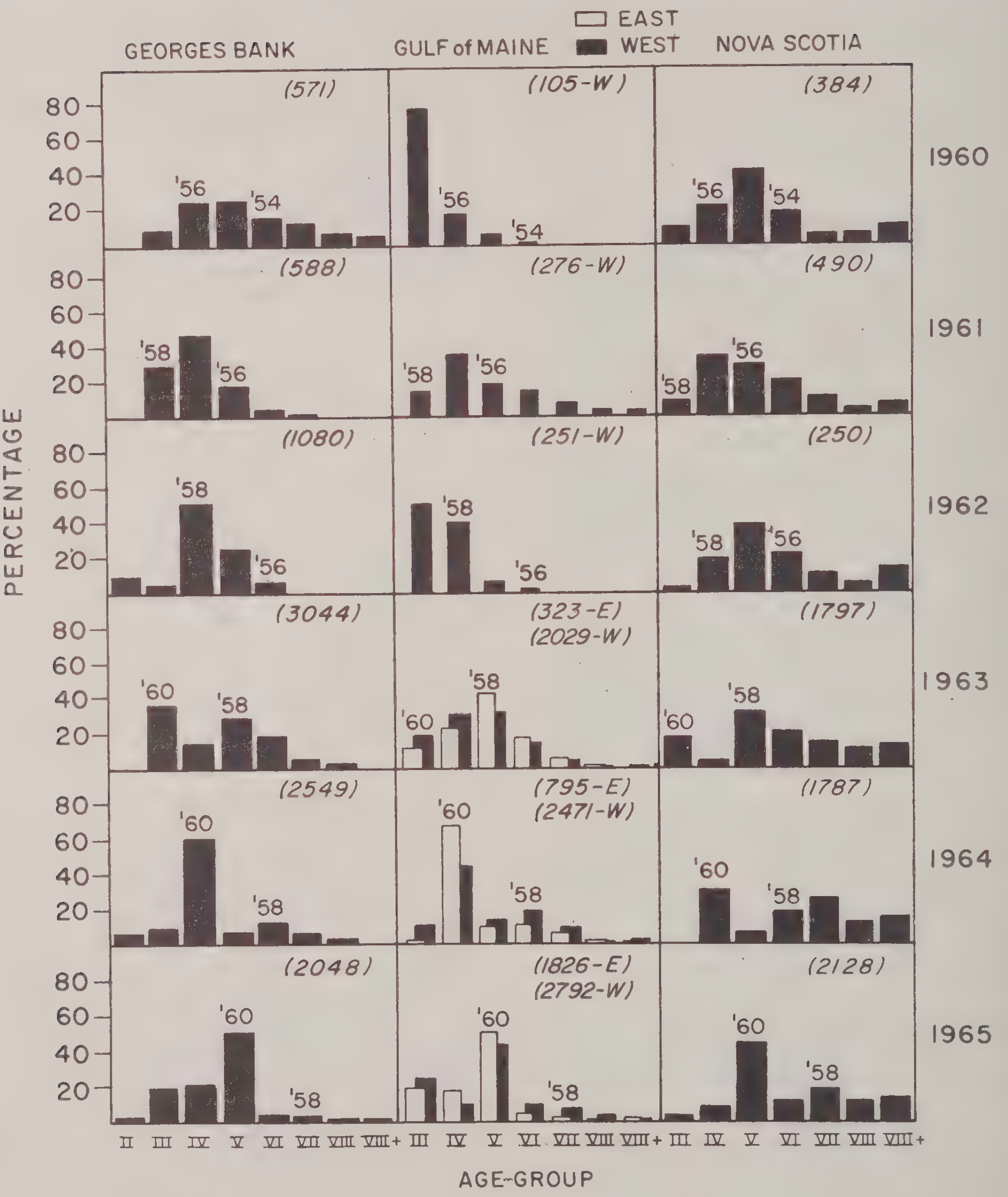

Fig. 2. Age and year-class composition of herring from Georges Bank, coastal Gulf of Maine, and Nova Scotia, 1960–65. Numbers of fish in parentheses.

Fish were measured from the tip of the lower jaw to the end of the longest lobe of the tail, with the fish lying in a natural position (natural total length). When the tail was damaged, fish were measured from the tip of the lower jaw to the silvery area on the caudal peduncle (standard length), and the length was converted to natural total length (TL = 2.80 + 1.157 SL where SL = standard length in millimeters). Length data, recorded to the nearest millimeter, have been grouped into 1-cm intervals.

Georges Bank

In 1960–65, age-group IV was dominant in the samples, followed in abundance by age-groups V, III, and VI. (Fig. 2). The highest frequency of occurrence of age-group IV was in 1964 (1960 year-class). The 1960 year-class entered the fishery in 1962 when it ranked third in percentage occurrence; in 1963–65 it ranked first. The 1960 year-class belonged to age-group II in 1962, age-group V in 1965. The 1960 year-class was not dominant or was absent from occasional samples taken in areas away from the Banks. In a sample from 40°46′N lat, 67°50′W long (June 1964), the 1958 and 1957 year-classes formed 61% of the sample, and the 1960 year-class, 24%. In a sample from 41°04′N lat, 66°12′W long (June 1965), the 1958 and 1957 year-classes formed 75% of the sample and the 1959 and older year-classes, 25%; the 1960 year-class was not represented. In a sample from the Northeast Peak in August 1964, the 1959 and 1958 year-classes accounted for 50% of the sample; the 1960 year-class, 25%. It seemed evident from the above samples, that the fish schooled according to age and to size.

The distribution of immature fish appeared to be restricted to the Banks proper, and the samples in which they dominated the catch were obtained from the vicinity of Cultivator and Georges Shoals and Northeast Little Georges. Immature herring were not caught farther east than Georges Shoals. Apparently these fish prefer the shallow areas (20 fathoms or less) of the Banks during the summer and early autumn, possibly because the bottom temperatures are higher than in the deeper areas as shown below.

Month and year	Range in temperature (°C)	
	Shallow water	Deeper water
June 1964	9.2–9.8	3.0–8.2
October 1964	13.1–15.1	4.8–13.1
September 1965	11.0	2.4–5.4

Comparable data are not available for Coastal Gulf of Maine and Nova Scotia.

The length of fish of each age-group increased from late spring through the summer, but during spawning season, the mean lengths of a particular age-group were frequently equal to or even less than the mean lengths before the spawning season. The apparent decrease of length in some samples can be explained on the assumption that the larger fish of an age-group spawn first, move off the spawning grounds, and are replaced by the smaller fish of the age-group. The dominance of the smaller fish of age-groups persists in the samples throughout the first few months of the following year. The last of the autumn spawning occurs at this time.

The mean length of a given age-group collected in August–September did not vary more than 1 cm, among the year-classes, except for the III-group fish (Table 3). The average increase in annual length from the III- to the IV-group fish was 2.8 cm; from the IV- to the V-group, 1.6 cm; and from the V- to the VI-group fish, 1.3 cm.

Coastal Gulf of Maine

Evidence supports a separation of eastern and western stocks of herring along the Gulf of Maine. Sindermann (1959) reported differences among parasites of herring in the eastern and western areas, and Sherman (1966) found differences in hydrographic conditions and abundance of zooplankton. On the basis of these differences, I have also divided herring samples from the Coastal Gulf of Maine into western and eastern groups. In 1960–65, herring of age-group V

TABLE 3. Mean lengths (cm) of herring of various age-groups and year-classes from Georges Bank in August–September, 1960–65.

Year-class	Year of capture					
	1960	1961[a]	1962	1963	1964	1965
1956						
Age-group	IV	V	VI	VII	VIII	—
Length	27.6	29.3	30.6	31.4	33.0	—
1957						
Age-group	III	IV	V	VI	VII	VIII
Length	25.6	27.8	29.3	30.4	32.1	33.3
1958						
Age-group	—	III	IV	V	VI	VII
Length	—	24.9	27.8	29.4	30.6	32.0
1959						
Age-group	—	—	III	IV	V	VI
Length	—	—	25.5	27.9	29.4	30.8
1960						
Age-group	—	—	—	III	IV	V
Length	—	—	—	24.3	27.3	28.9
1961						
Age-group	—	—	—	—	III	IV
Length	—	—	—	—	23.7	27.1

[a] Only data available were for October.

dominated the samples in both sections (Fig. 2). The order for other major age-groups was IV, III, and VI in both sections. The dominant year-class was always more abundant in the eastern section than in the western section. In both sections the 1960 year-class was first evident in the samples in 1963 (age-group III) and was dominant in 1964 and 1965 (age-groups IV and V). The relative abundance of fish of the 1959 year-class was greater along western and eastern Coastal Gulf of Maine than on Georges Bank. In 1963 and 1965 fish of the dominant year-class were plentiful in all samples. A few 1964 samples from Provincetown, Massachusetts, and Boothbay Harbor, Maine, were dominated by fish of the 1958 and 1959 year-classes, and fish of the 1960 year-class made up less than 10% of the collections.

The length frequencies of fish from the western and eastern sections were similar in 1965 and 1963, but in 1964 differences between lengths of fish from these sections were highly significant. The mean length of fish of an age-group collected in August–September did not vary more than 1 cm among year-classes, except for IV-group fish from the eastern section (Table 4). In the western section, the average increase in annual length from III- to the IV-group fish was 2.7 cm; from IV- to the V-group, 1.3 cm; and from V- to the VI-group, 1.4 cm. In the eastern section, the average increase in length from IV- to the V-group was 1.4 cm; and from V- to the VI-group, 1.5 cm.

Nova Scotia

Herring of age-group V were dominant in the samples in 1960–65 (Fig. 2) followed in percentage occurrence by age-groups VII, VI, and IV. Fish in age-groups V and VIII were more abundant in the samples than fish in age-group IV, except in 1961 and 1964. The 1960 year-class which ranked third in abundance in 1963 (age-group III) was dominant in 1964 and 1965. In general, the samples from Nova Scotia contained a higher percentage of older fish than the samples from either Georges Bank or the Gulf of Maine. The 1959 year-class, as on Georges Bank, was noticeably weak.

Although the 1960 year-class contributed 43% of all fish collected in 1965, some samples from St. Mary's Bay, Port Mouton, and Lockeport contained less than 10% of this year-class. Fish of the 1958 and 1957 year-classes were abundant in these collections. In 1964, the

TABLE 4. Mean lengths (cm) of herring from various age-groups and year-classes from Coastal Gulf of Maine in August–September, 1960–65 (W—Western Section, E—Eastern Section).

	Year of capture											
	1960		1961		1962[a]		1963		1964		1965	
Year-class	W	E	W	E	W	E	W	E	W	E	W	E
1956												
Age-group	IV	—	V	—	VI	—	VII	VII	VIII	VIII	—	—
Length	27.7	—	29.4	—	30.2	—	31.9	32.1	33.4	33.1	—	—
1957												
Age-group	III	—	IV	—	V	—	VI	VI	VII	VII	VIII	VIII
Length	25.0	—	28.2	—	29.2	—	30.8	30.5	32.0	32.1	33.2	33.0
1958												
Age-group	—	—	III	—	IV	—	V	V	VI	VI	VII	VII
Length	—	—	25.7	—	27.4	—	29.5	29.0	30.8	30.6	31.9	32.0
1959												
Age-group	—	—	—	—	III	—	IV	IV	V	V	VI	VI
Length	—	—	—	—	25.3	—	28.0	27.9	29.6	29.6	30.9	30.8
1960												
Age-group	—	—	—	—	—	—	III	III	IV	IV	V	V
Length	—	—	—	—	—	—	25.2	23.1	27.8	26.6	29.2	28.9
1961												
Age-group	—	—	—	—	—	—	—	—	III	—	IV	IV
Length	—	—	—	—	—	—	—	—	23.6	—	27.5	26.8

[a] Only data available were for October.

TABLE 5. Mean lengths (cm) of herring of various age-groups and year-classes from Nova Scotia in August–September, 1960–65.

	Year of capture					
Year-class	1960	1961	1962	1963	1964	1965
1956						
Age-group	IV	V	VI	VII	VIII	—
Length	27.7	29.5	30.9	32.1	33.0	—
1957						
Age-group	—	IV	V	VI	VII	VIII
Length	—	27.9	29.1	30.8	32.0	33.4
1958						
Age-group	—	—	IV	V	VI	VII
Length	—	—	27.2	29.2	30.7	32.1
1959						
Age-group	—	—	—	IV	V	VI
Length	—	—	—	27.2	29.6	30.9
1960						
Age-group	—	—	—	III	IV	V
Length	—	—	—	23.7	26.4	28.9
1961						
Age-group	—	—	—	—	—	IV
Length	—	—	—	—	—	27.2

1960 year-class was dominant, but some samples from Port Mouton, Lockeport, and Pubnico were dominated by the 1957 and 1958 year-classes. The 1958 year-class dominated the samples in 1963, but some samples from Trinity Ledges, Carleton Village, and Yarmouth were dominated by the 1960, 1957, or 1956 year-classes.

The range in lengths of herring of the various year-classes collected in August–September varied little from year to year. The mean length of fish for any age-group did not vary more than 1 cm, except for IV-group fish (Table 5). The average increase in length from age-group IV- to the V-group was 2.0 cm; from V- to the VI-group, 1.5 cm.

Stages of Maturity

Most herring from Georges Bank, Coastal Gulf of Maine, and Nova Scotia are mature at age-group IV, although in some years large percentages of fish may mature at age-group III (Table 6). The length of the fish at the time of its first spawning did not differ appreciably between the sexes. Scattergood (1952) reported the same for the herring he examined and stated, "there seems to be no reason to believe that the size at maturity is markedly different between males and females." Although the lengths of fish at the time of their first spawning varied slightly from year to year and from area to area, in general, fish of age-group III which had matured were approximately 26.0 cm long. Fish of age-group IV which had matured were approximately 27.5 cm long. The fish of age-group IV which had not matured and which would not spawn until the following year were usually less than 27.0 cm long.

TABLE 6. Percentage of mature herring for age-groups III and IV collected during the spawning season from Georges Bank, Coastal Gulf of Maine, and Nova Scotia, 1960–65.

	Georges Bank		Coastal Gulf of Maine		Nova Scotia	
	Age-group		Age-group		Age-group	
Year	III	IV	III	IV	III	IV
1960	62	97	2	79	—	100
1961	6	87	0	92	—	95
1962	56	95	15	66	—	91
1963	33	97	27	96	7	100
1964	9	93	1	92	—	84
1965	10	79	7	70	0	94

Data on state of gonads pooled for 1960–65 were compared by month for each of the three areas. The maturity scale proposed by the International Council for the Exploration of the Sea in 1963 and adopted by ICNAF in 1964 was used in the classification of the various gonadal stages (Table 7). Eight stages of gonadal development were recorded, but to simplify the comparison, the stages were grouped into four categories: II and III — Maturing; IV and V — Full; VI and VII — Spawning and Recently Spent; and VIII — Recovering Spent. Fish of stage I were omitted from the comparisons.

TABLE 7. Gonadal stages and the description of the gonads and eggs of herring in the various stages.[a]

Stage	Description
I	Virgin herring. Gonads very small, threadlike, 2–3 mm broad. Ovaries wine red. Testes whitish or grey brown.
II	Virgin herring with small sexual organs. The height of ovaries and testes about 3–8 mm. Eggs not visible to the naked eye but can be seen with magnifying glass. Ovaries a bright red colour; testes a reddish grey colour.
III	Gonads occupying about half of the ventral cavity. Breadth of sexual organs between 1–2 cm. Eggs small but can be distinguished with naked eye. Ovaries orange; testes reddish grey or greyish.
IV	Gonads almost as long as body cavity. Eggs larger, varying in size, opaque. Ovaries orange or pale yellow; testes whitish.
V	Gonads fill body cavity. Eggs large, round; some transparent. Ovaries yellowish; testes milkwhite. Eggs and sperm do not flow, but sperm can be extruded by pressure.
VI	Ripe gonads. Eggs transparent; testes white; eggs and sperm flow freely.
VII	Spent herring. Gonads baggy and bloodshot. Ovaries empty or containing only a few residual eggs. Testes may contain remains of sperm.
VIII	Recovering spents. Ovaries and testes firm and larger than in virgin herring in stage II. Eggs not visible to naked eye. Walls of gonads striated; blood vessels prominent. Gonads wine red colour. (This stage passes into stage III.)

[a] Descriptions are verbatim from the official ICNAF definition.

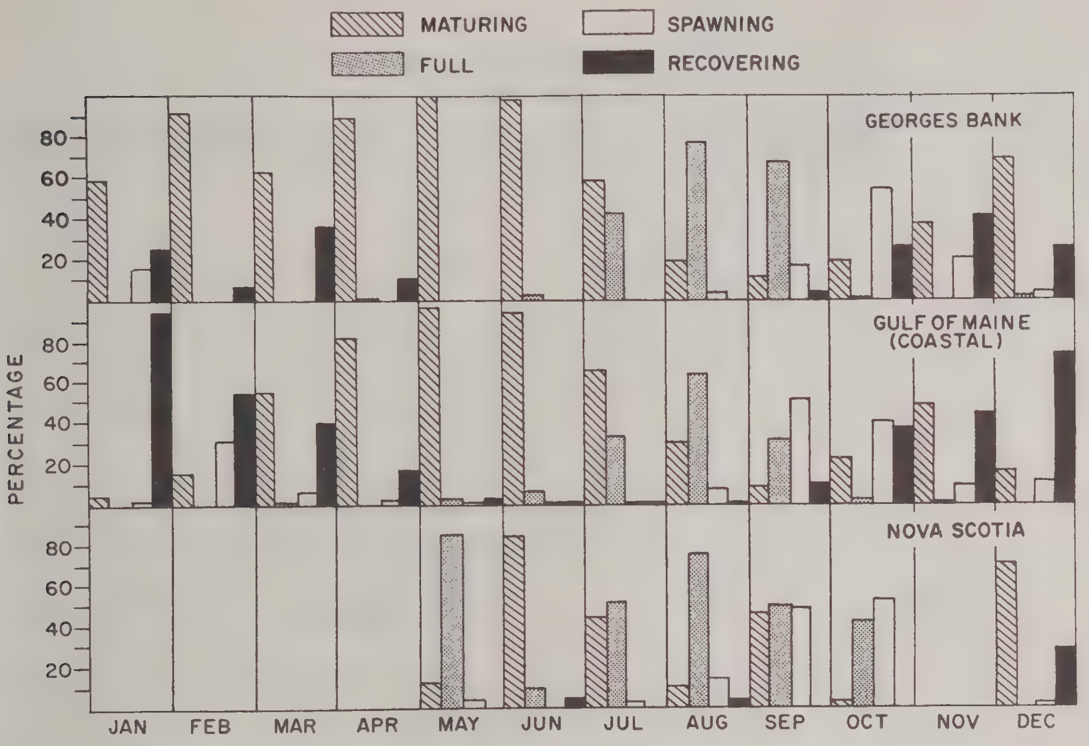

Fig. 3. Annual trend in gonadal stages of herring from Georges Bank, coastal Gulf of Maine, and Nova Scotia, 1960–65 (pooled data).

Georges Bank

During the first 7 months of the year most herring were maturing (Fig. 3). The percentage of maturing fish decreased in August and reached a minimum in September. The number of maturing fish increased gradually from late October through December due to an influx of virgin herring. The first full fish were taken in April; they reached their peak by August, and decreased during September and October. Spawning began in the latter part of August and yolk-sac larvae were first collected in September. The percentage occurrence of spawning fish increased through September. Spawning and recently spent fish were usually in the majority during October and were still present in January. Recovering spent fish were first collected in September and numbers increased during the late autumn. Recovering spent fish also were collected from January to April.

Coastal Gulf of Maine

As on Georges Bank, most herring were maturing during the first 7 months of the year (Fig. 3). Full fish, first taken in March, increased through July, and reached their maximum frequency by August. The number declined sharply in September and only a few full fish were caught in October and November. The capture of a few spawning fish (less than 2% of those sampled) from Eastport, Maine, and Cape Cod, Massachusetts, during the spring and early summer indicates some spring spawning. The percentage of spawning fish in the monthly samples was highest in September in 1964 and 1965 and in October in 1963. The onset of spawning was during August in 1964 and 1965, and in September in 1963. The percentage of spawning fish decreased from November through March. The collection of recovering spent fish during most months provided additional evidence of limited spring spawning in the coastal waters.

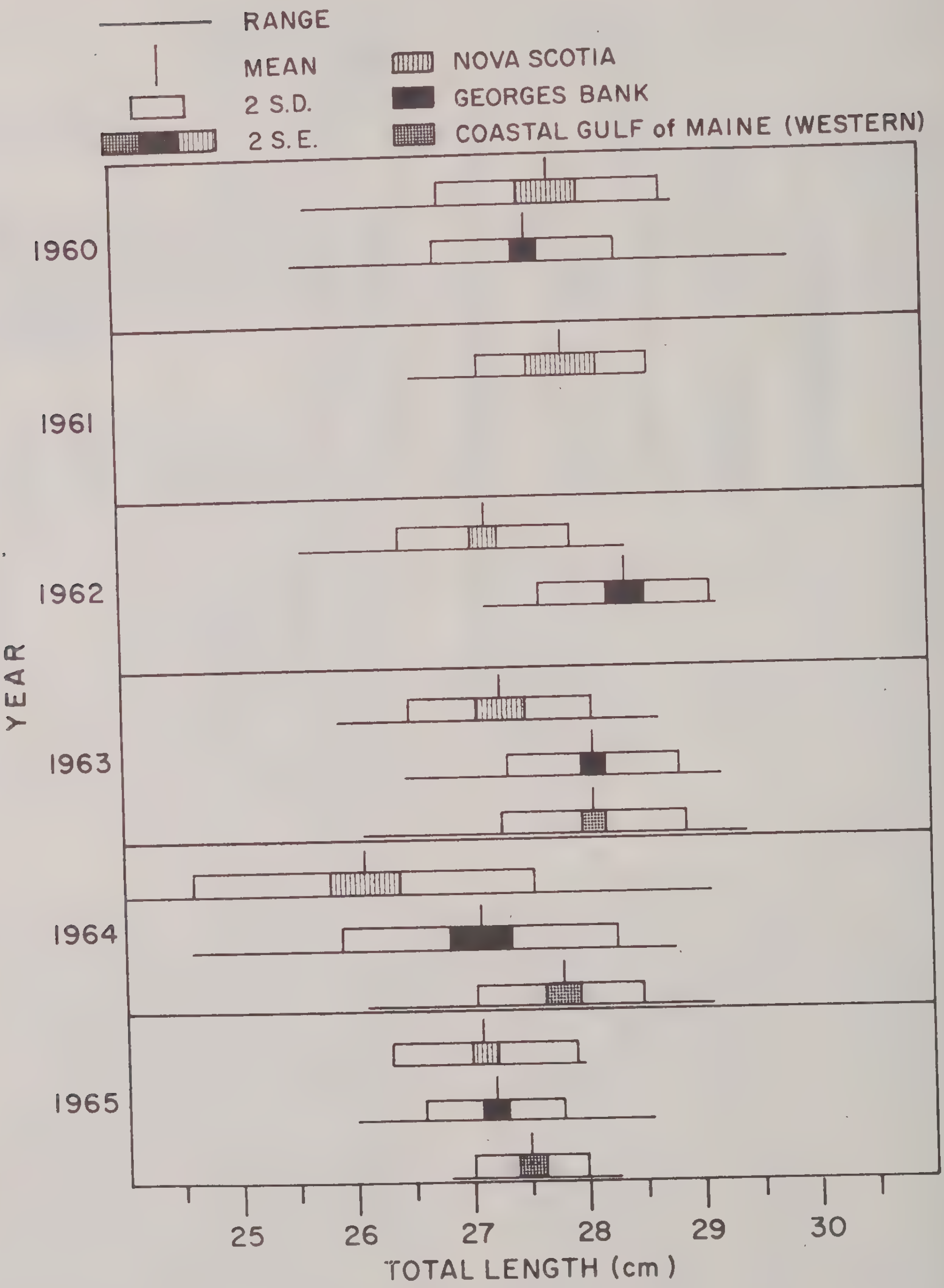

Fig. 4. Lengths of herring of age-group IV from Georges Bank, coastal Gulf of Maine and Nova Scotia in August, 1960–65.

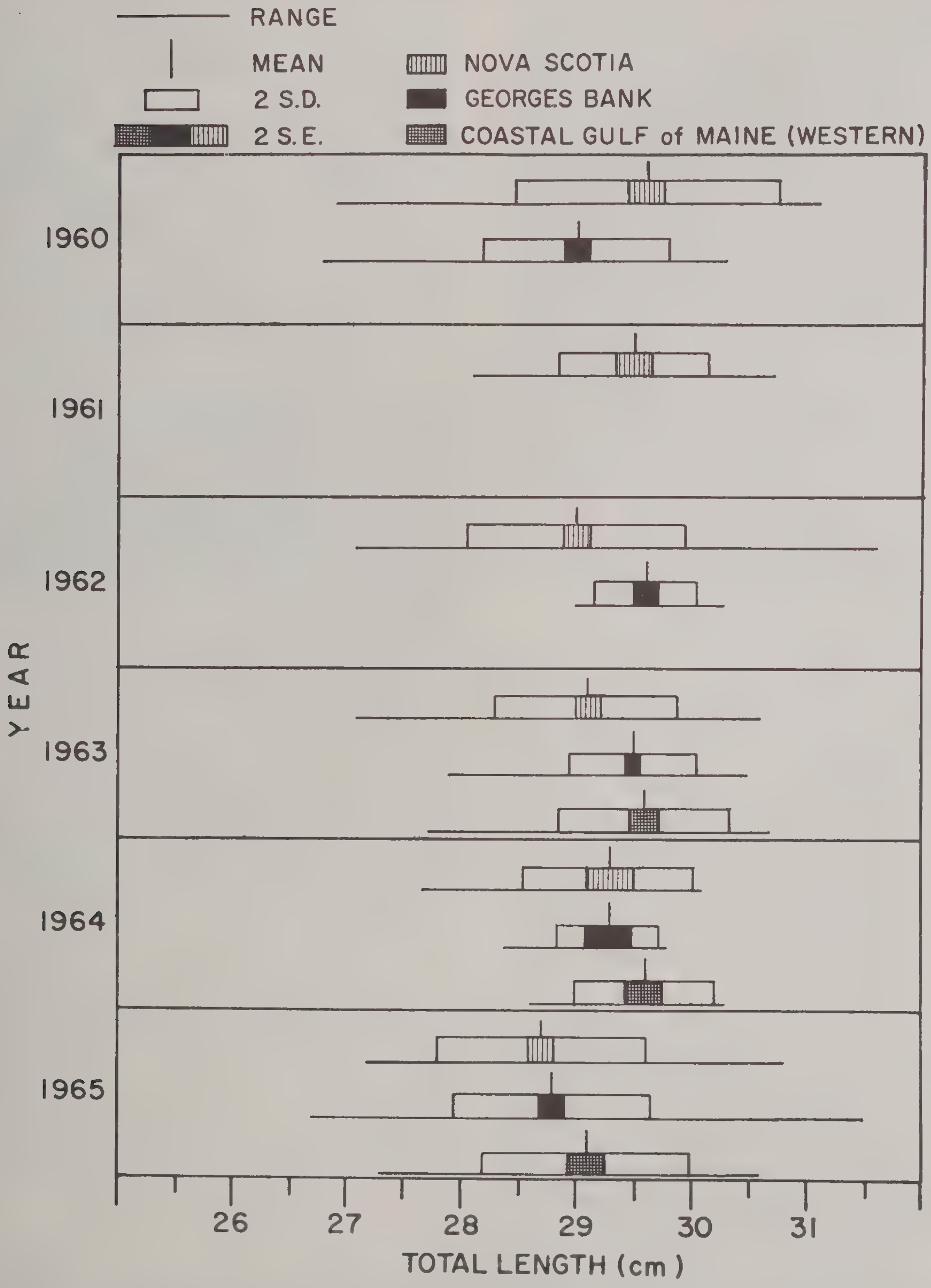

Fig. 5. Lengths of herring of age-group V from Georges Bank, coastal Gulf of Maine, and Nova Scotia in August, 1960–65.

Nova Scotia

Most samples from Nova Scotia were collected from May to October (Fig. 3). Most fish were maturing in June, and by August the percentage of mature fish had decreased considerably. Full fish were first collected in May, and predominated in July and August. The capture of a few spawning fish in late spring and early summer suggests some spring-summer spawning. Autumn spawning began in August, and as indicated by the percentage of full fish in September, reached its peak during October. A few recovering spent fish taken in September provide additional evidence that the peak of spawning came later than September. The high incidence (over 80%) of full fish (stage V) in the sample of May 1962 suggests that these fish would have spawned in the spring. These fish were taken from St. Mary's Bay. The presence of several fish in stage VIII in July samples indicates that they had spawned sometime in the spring.

Comparison of Maturity, Age, and Length Frequency Distributions

Even before the start of the extensive offshore fishery on Georges Bank, biologists in the Northwest Atlantic were interested in the relationships among the populations of herring from Georges Bank and the Gulf of Maine (Tibbo *et al.*, 1958; Sindermann, 1959; Colton and Temple, 1961). Basic information on the biology of adult herring from Nova Scotia had been documented (Tibbo, 1957), but knowledge about adult herring from Georges Bank and the Coastal Gulf of Maine, until recent years, had been almost negligible. The present report, based on herring collected in 1960–65, provides additional information on the biology of adult herring from these areas.

The IV- and V-group fish dominated the samples in the three areas for every year except 1963, when age-group III was dominant on Georges Bank and in 1960 and 1962 when age-group III was dominant in the Coastal Gulf of Maine. The 1960 year-class dominated the samples in the three areas in 1965 and 1964. The 1960 year-class was dominant on Georges Bank in 1963 and the 1958 year-class was dominant in the Coastal Gulf of Maine and Nova Scotia. In 1962, the 1958 year-class dominated on Georges Bank, the 1957 year-class in Nova Scotia, and the 1959 year-class in the Coastal Gulf of Maine. The 1957 year-class dominated the samples from all three areas in 1961. In 1960, the 1955 year-class was dominant on Georges Bank and off Nova Scotia, but the 1957 year-class dominated the samples from Coastal Gulf of Maine.

The mean lengths of fish from the 1960 year-class in August 1964 and 1965 were less than the mean lengths of age-groups IV and V collected in the other years, except for age-group IV from the Coastal Gulf of Maine in 1965 (Fig. 4 and 5). The mean lengths of age-groups IV and V from the Coastal Gulf of Maine were consistently greater than those of fish of the same age from Georges Bank; the Georges Bank fish, except in 1960, were longer than fish from Nova Scotia.

The mean lengths of fish of the 1960 year-class were generally smaller than those of fish of the same age from other year-classes. Because the 1960 year-class was dominant in many samples, the growth may be density-dependent. The 1959 year-class which dominated the samples in Coastal Gulf of Maine during 1962 and ranked second in occurrence in 1963 was extremely weak in the other two areas. In no year did it rank higher than fourth in either Georges Bank or Nova Scotia.

Differences in spawning time of herring were slight. From 1960 through 1965, herring from Georges Bank and Nova Scotia began to spawn in August; in Coastal Gulf of Maine, the spawning began either in August or September. The peak of spawning on Georges Bank and Nova Scotia always came in October. The peak of spawning in Coastal Gulf of Maine was in October in some years, and September in others. Evidence is lacking for any spring spawning on Georges Bank, but a few spring spawners were collected in Coastal Gulf of Maine and in Nova Scotia.

The differences in age composition and length of fish of a given year-class and the slight differences in spawning time, along with the obvious geographic separation of the three spawning stocks studied, suggest that the stocks may be independent subpopulations. Before conclusions can be reached as to the discreteness of each spawning stock, data from meristic characters and other racial information must be analyzed.

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POPULATION CHARACTERISTICS AND PHYSICAL CONDITION OF ALEWIVES, *ALOSA PSEUDOHARENGUS*, IN A MASSIVE DIEOFF IN LAKE MICHIGAN, 1967[1]

Edward H. Brown, Jr.

ABSTRACT

The length, age and sex compositions of dead and dying alewives collected in June 1967 at six locations in southern, central, and northern Lake Michigan are compared with those of fish taken in experimental trawls at five locations in April and June 1967. Behavior at the time of death, condition of the body and gonads, stomach contents, and the incidence of *Saprolegnia* and subcutaneous hemorrhages also are described for alewives in the dieoff.

The length distributions of alewives in the dieoff and trawl collections were similar and bimodal. Yearlings made up 25 and 42 percent of the respective collections. The average ages of adults (age-group II and older) were nearly identical in the dieoff and trawl collections (3.5 and 3.6 years, respectively). Both collections were dominated by age-groups III and IV. The average lengths of adult alewives in age-groups II to V in the dieoff were smaller than or identical to those in the trawl collections. In all collections females were consistently older (0.4 year) than the males and larger at the greater ages. The sexes were almost equally represented among age-II and older fish in the dieoff.

Despite the presence of *Saprolegnia* and hemorrhages on some fish, alewives in the dieoff appeared robust. Spawning attrition could not have been a major cause of the dieoff because many immature yearlings died and 80 percent of the dead adults were unspawned. The presence of rapidly digestible zooplankton in the stomachs of dead alewives indicated that many fish were feeding just before death. About 20 percent of the alewives in the selected samples of fish from the dieoff were infected by *Saprolegnia*; twice as many females were infected as males. The fungus was randomly distributed among the size groups. Hemorrhages may have been a symptom or physiological response to the cause of the dieoff because they affected a much higher percentage of the dying alewives (47 percent) than did fungus. Occurrence of the hemorrhages did not differ significantly between the sexes or among the size groups.

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[1] Contribution No. 377, Ann Arbor Biological Laboratory, U. S. Bureau of Commercial Fisheries.

Introduction

After the first record of its occurrence near South Manitou Island in 1949 (Miller, 1957), the alewife spread throughout Lake Michigan; its abundance increased tremendously during the 1960's. The classic population explosion, which crested in the southern and central basins of the lake in 1966 (Fig. 1), was accompanied by progressively heavier spring and summer dieoffs and was climaxed by a massive mortality in June and early July 1967. The 1967 dieoff was in progress by the first week of June and reached its greatest intensity by the third week, when huge windrows of fish were deposited by wind and waves on beaches in Michigan, Indiana, Illinois, and Wisconsin.

An aerial survey on June 22 revealed that the alewife dieoff extended around the circumference of the lake from Arcadia, Michigan, south to Michigan City, Indiana, and along the west shore to Sturgeon Bay, Wisconsin (Fig. 2). Dead alewives were also seen along the east shore of Green Bay,

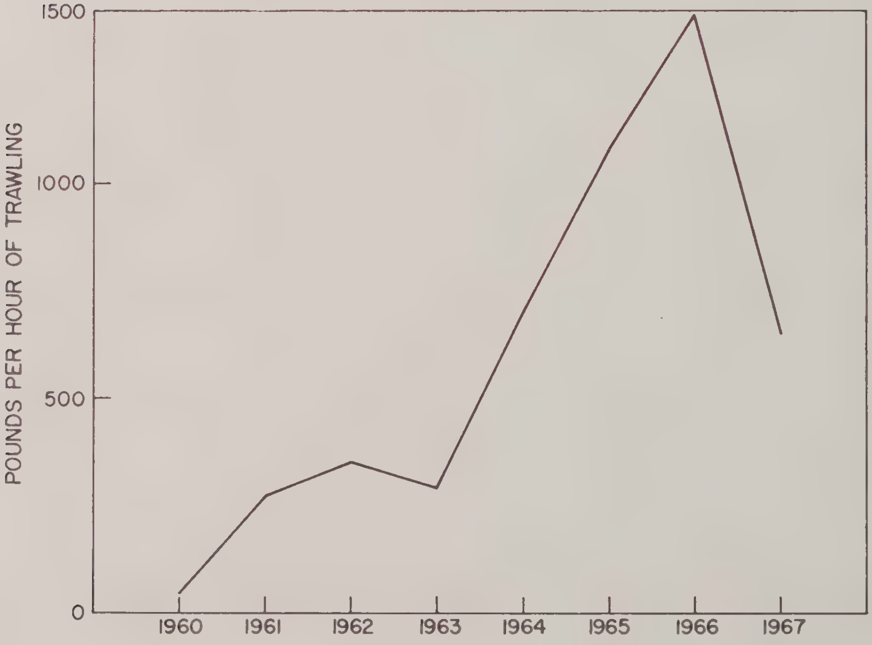

Figure 1. Relative abundance of adult alewives taken in experimental and Commercial bottom trawls in southern and central Lake Michigan, November 1960-67.

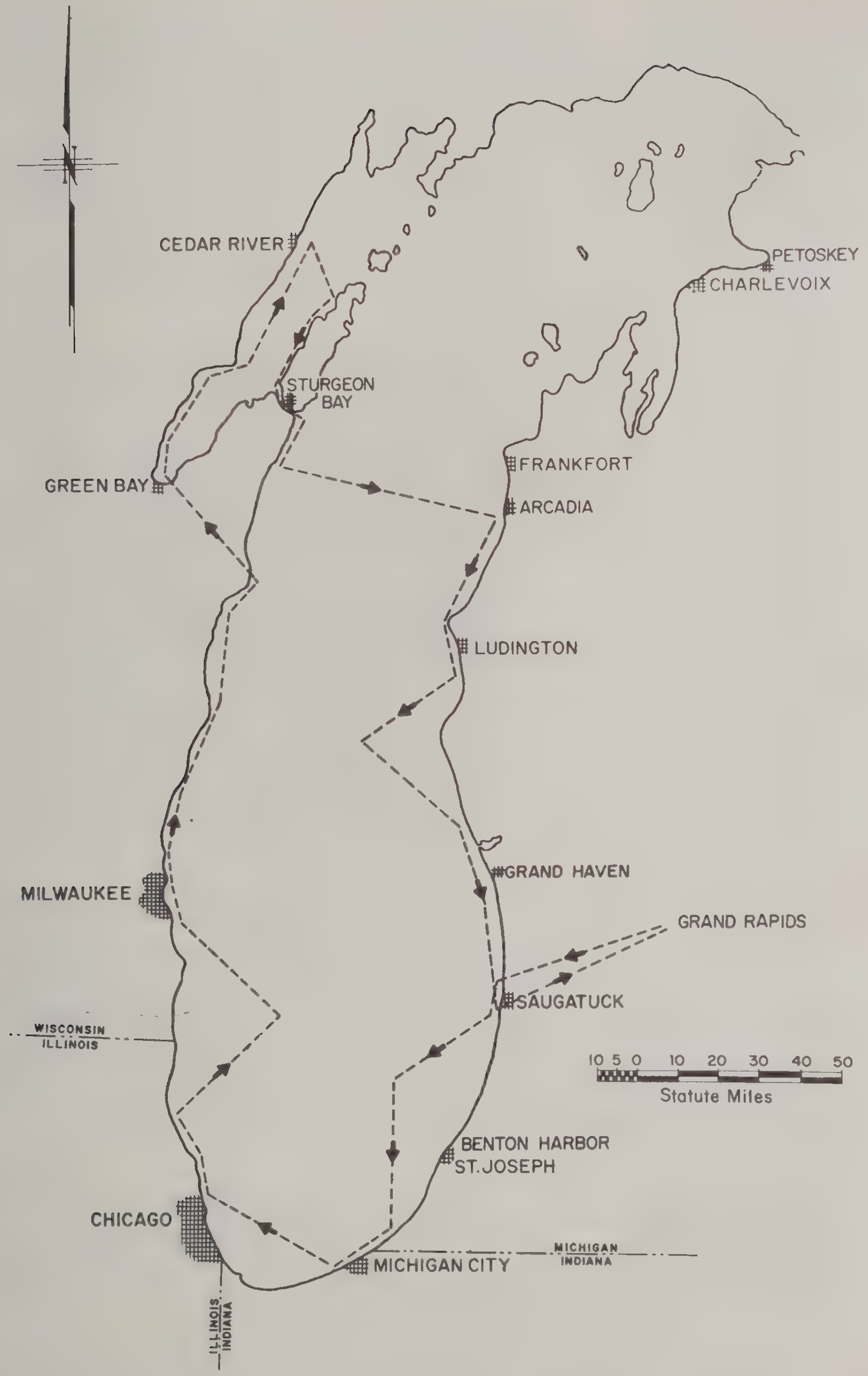
CEDAR RIVER
PETOSKEY
CHARLEVOIX
STURGEON BAY
GREEN BAY
FRANKFORT
ARCADIA
LUDINGTON
GRAND HAVEN
MILWAUKEE
GRAND RAPIDS
SAUGATUCK
WISCONSIN
ILLINOIS
10 5 0 10 20 30 40 50
Statute Miles
BENTON HARBOR
ST. JOSEPH
CHICAGO
MICHIGAN
INDIANA
MICHIGAN CITY
ILLINOIS
INDIANA

Figure 2. Sampling locations and route (broken line) of the airplane survey of June 22.

and a northward extension of the dieoff was reported at Charlevoix and Petoskey, Michigan. Dead alewives were mostly concentrated within 1 mile of shore and gradually disappeared toward midlake. The accumulation of dead fish was greatest from Benton Harbor, Michigan, to Chicago, Illinois, and was heavier along the Michigan shore of the central basin than along the Wisconsin shore. Prevailing winds, currents, and changes in wind direction affected the daily concentrations of dead fish, and undoubtedly contributed to the vast concentrations at Chicago.

The annual spring and summer dieoff of alewives coincides to some extent with the annual inshore migration in April and May and the subsequent movement into tributaries where alewives spawn from late May to mid-August. Extensive dieoffs in April-August have been observed in Lake Huron in recent years and in Lake Ontario since the early appearance of the fish in the late 1800's (Miller[2]; Graham, 1956).

The alewife encounters sharp changes in water temperature between the deep, cold waters of the Great Lakes and the shallow, warmer waters inshore and in the tributaries. The possible inability of the fish to adapt to severe temperature changes is one of the more plausible explanations suggested for the mortalities. In Lake Ontario Graham (1956) correlated daily mortalities with water temperature gradients that were intensified by still days and rising air temperatures.

A physiological malfunction that may be triggered by environmental change to cause catastrophic death of the alewife remains to be identified. Hoar (1952) suggested that fish may lose osmotic control in warm water through an exhausted thyroid mechanism possibly related to low iodine in freshwater. It is not known, however, if the thyroid gland has an osmoregulatory function in fish (Pickford and Atz, 1957), but it may influence other important physiological functions of the alewife.

Algal toxicity was recently suggested as the possible cause of the dieoff. Williams (1968) contended that the 1967 mass mortality " . . . appears to be related to a bloom of toxic blue-green algae and is not simply the result of the alewife's instinctive behavior and lack of ability to adapt to new lake conditions . . . . '' Alewives were abundant after the dieoff, however, in areas where blue-green algae thrive.

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[2] Miller, G. W. 1930. The mortality of alewives (*Pomolobus pseudoharengus* Wilson) in Lake Ontario. Univ. of Toronto, Ont. Fish. Res. Lab. Manuscript 47p.

The present report documents the 1967 dieoff--an event of great public concern--and provides background information for further research needed to explain the annual phenomenon.

Methods

Dead and dying alewives were collected randomly in dip nets from the surface of inshore waters off Michigan City, Indiana; St. Joseph, Saugatuck, Ludington, and Frankfort, Michigan; and Sturgeon Bay, Wisconsin, on June 9 and 27-29, 1967 (Fig. 2). The earliest sampling (June 9) was at Frankfort from a public dock inside the mouth of the Betsie River. The samples at Michigan City were netted from small boats near beaches north and south of the breakwall on June 28 and 29. The sample at St. Joseph was obtained on June 29 by dipping fish just off a public beach near the breakwall. Fish were collected by the R/V *Kaho* at the southern end of Sturgeon Bay (June 27) and at the mouths of the breakwalls at Ludington (June 28) and Saugatuck (June 29).

Fish were preserved in formalin or frozen and later examined at the Ann Arbor Biological Laboratory. The total length of each fish was recorded in millimeters and most of the adults were weighed to the nearest gram and sexed. Sex could not be determined for age-I fish. Scales for age determination were removed from an area 4-5 scale rows below the insertion of the dorsal fin. The number of fish used for age determination and sex composition varied according to the number available or the number needed for the various analyses. Age groups are designated by Roman numerals corresponding to the number of completed annuli. All the fish were considered to have passed into the next higher age group on January 1.

The condition of the gonads of age-II and older alewives from the dieoff at Saugatuck, Ludington, and Sturgeon Bay was determined by dissection. The gonads of frozen fish retained most of their natural color and surface texture, which is broadly diagnostic of spawning condition.

The incidences of fungus infection (*Saprolegnia*) and subcutaneous hemorrhaging, common among the dieoff alewives, were recorded for dying fish taken north of the breakwall at Michigan City and at St. Joseph.

The length, sex, and age compositions of fish in the dieoff were compared with those of alewives taken in experimental trawls at the following locations and dates: Saugatuck, April 13; Grand Haven, April 16; Benton Harbor, April 19; Sturgeon Bay (Lake Michigan side), June 9; and Frankfort, June 11. The trawls were of the North Atlantic whiting design and had 39-foot head ropes, 2-1/2- to 2-inch-mesh bodies, and 1/2-inch-mesh cod ends (stretched measure). The trawls were fished on the bottom along the contour at depths of 3 to 50 fathoms.

Behavior of Dying Fish

The behavior of dying alewives was observed on the afternoon of June 9 at Frankfort and June 28 at Michigan City. The stricken fish swam weakly on their sides in vertical spirals that brought them to the surface. Some exerted sudden bursts of swimming effort and were propelled sideways or downward. Their attempts to regain equilibrium lasted several seconds before they again rose to the surface where they quivered and died. All sizes of alewives died side by side and behaved in the same manner. The behavior of the dying fish in Lake Michigan agrees closely with accounts given for Lake Ontario by Miller[2] and Graham (1956).

Length Composition

The length distributions of alewives in the dieoff and trawl collections were similar and bimodal—a lower mode for yearlings and an upper mode for older fish (Table 1). The discontinuity or dip in the individual frequencies fell near 120 mm, which was the arbitrary length used to separate yearlings from adults ($\geqslant$ 120 mm). The average length of yearling alewives was greater in the combined dieoff samples (88 mm) than in the trawl collections (81 mm), but the average length of adults in the respective collections were nearly identical (161 and 162 mm). In five dieoff and trawl collections that came from the five general areas (Michigan City-Benton Harbor-St. Joseph, Saugatuck, Grand Haven-Ludington, Frankfort, and Sturgeon Bay), yearlings from the dieoff were longer than those from trawls in four, but the adults from the

Table 1. Length distributions of alewives taken in bottom trawls and from the dieoff at various locations in Lake Michigan, April and June 1967

Total length (millimeters)	Trawls[1]					Dieoff							
	Benton Harbor April 19	Saugatuck April 13	Grand Haven April 16	Frankfort June 11	Sturgeon Bay June 9	Michigan City June 28-29	St. Joseph June 29	Saugatuck June 29	Ludington June 28	Frankfort June 9	Sturgeon Bay June 27	Trawl total	Dieoff total
50-59	2	-	2	3	-	-	-	-	-	-	-	7	-
60-69	8	3	14	162	116	1	1	-	4	4	-	303	10
70-79	14	5	33	646	731	24	9	1	18	6	3	1,429	61
80-89	30	7	38	251	613	38	18	4	28	5	2	939	95
90-99	19	2	23	105	320	19	27	2	16	8	4	469	76
100-109	22	-	6	23	112	9	10	2	18	1	2	163	42
110-119	5	-	4	3	54	7	-	-	1	1	2	66	11
120-129	20	4	16	8	58	3	-	2	1	-	1	106	7
130-139	58	12	39	24	138	11	1	5	5	5	11	271	38
140-149	155	47	92	32	240	32	15	14	17	13	28	566	119
150-159	310	132	190	75	296	70	36	18	44	8	63	1,003	239
160-169	453	240	232	162	274	80	44	27	53	8	56	1,361	268
170-179	342	181	129	112	141	44	29	22	42	2	20	905	159
180-189	152	87	51	52	49	9	6	9	13	6	11	391	54
190-199	43	22	14	10	12	1	-	3	3	-	-	101	7
200-209	8	4	3	1	-	-	-	-	-	-	-	16	-
210-219	-	2	-	1	3	-	-	-	-	-	-	6	-
230-234	-	-	-	-	1	-	-	-	-	-	-	1	-
Total fish	1,641	748	886	1,670	3,158	348	196	109	263	67	203	8,103	1,186
Average length	159	165	150	102	111	139	138	156	139	129	154	128	143
Percentage yearlings	6	2	14	71	62	28	33	8	32	37	6	42	25
Average length yearlings	89	80	83	77	83	87	89	90	88	85	92	81	88
Percentage adults	94	98	86	29	38	72	67	92	68	63	94	58	75
Average length adults	164	167	161	164	155	160	162	162	163	155	158	162	161

[1] The catches of alewives in trawls were sorted into two groups—yearlings (less than 120 mm) and adults (120 mm or larger)—and counted. A subsample from each group was then measured to determine length-frequency distribution. For adults, the entire subsample for each locality is represented in the table. For yearlings, however, the numbers shown have been adjusted to preserve the ratio between the number of yearlings and number of adults in the total catch. The number of yearlings actually measured from catches at the various ports were: Benton Harbon, 127; Saugatuck, 53; Grand Haven, 153; Frankfort, 375; and Sturgeon Bay, 803.

dieoff were slightly smaller in three. Although growth of young alewives may start in late June, the dieoff was sampled only 2 days before the trawl collections at Frankfort in early June (9-11) and the dieoff fish were larger.

Comparisons between the percentages of yearlings in the dieoff and trawl collections are difficult because of large discrepancies between the percentages in the southern (2 to 14 percent) and northern (62 and 71 percent) trawl collections (Table 1). The differences in the trawl collections were undoubtedly caused by a change in the bathymetric distribution of alewives between mid-April and early June. Yearling alewives are widely scattered in April but in May and June the fish move shoreward and are more concentrated near the bottom. Also by late May and June many adults are close inshore or have entered streams to spawn and are not available to trawls. The percentage of yearling alewives from all locations combined was 25 percent in the dieoff and 42 percent in the bottom trawl collections.

Graham (1956) also found substantial numbers of yearling alewives in the dieoffs in the Bay of Quinte region of Lake Ontario. Biologists and fishermen from Lake Michigan reported, however, that yearlings were much better represented in the 1967 dieoff than in those of previous years.

Age Composition

The average ages of the adult alewives were nearly identical in the dieoff and trawl collections (3.5 and 3.6 years, respectively) and the average age of females exceeded that of males in every collection (Tables 2 and 3). Preliminary studies have shown that males mature earlier, are recruited at a younger age to the bottom stocks and to the spawning population, and die earlier than females. The females consequently averaged 0.4 year older than the males in both the trawl and dieoff collections.

Age-II alewives that mainly occupy midwater levels of the lake until midsummer and fall were scarce in the dieoff (5.5 percent for all ports) and trawl collections (4.3 percent). Most age-II fish are immature in the spring and early summer and these fish apparently do not enter the inshore waters or the tributaries in proportion to their numbers in the lake. During the 1965 spawning season, age-II alewives represented only 11 percent of the spawning fish in the Kalamazoo River

Table 2. Age composition (percentage) by sex of dead and dying adult alewives from six locations in Lake Michigan and Sturgeon Bay, June 1967

Location and date	Sex	Number of fish	Age group					Average age
			II	III	IV	V	VI	
Michigan City June 28-29	Male	79	2.5	57.0	36.7	3.8	-	3.4
	Female	75	1.3	48.0	44.0	6.7	-	3.6
	Combined	154	1.9	52.6	40.3	5.2	-	3.5
St. Joseph June 29	Male	75	5.3	66.7	22.7	5.3	-	3.3
	Female	54	-	40.7	46.3	13.0	-	3.7
	Combined	129	3.1	55.8	32.6	8.5	-	3.5
Saugatuck June 29	Male	44	13.6	52.3	29.6	4.5	-	3.2
	Female	56	1.8	41.1	46.4	10.7	-	3.7
	Combined	100	7.0	46.0	39.0	8.0	-	3.5
Ludington June 28	Male	55	5.5	69.1	23.6	1.8	-	3.2
	Female	86	3.5	28.7	44.8	20.7	2.3	3.9
	Combined	141	4.2	44.4	36.6	13.4	1.4	3.6
Frankfort June 9	Male	19	15.8	47.4	26.3	10.5	-	3.3
	Female	24	8.3	50.0	16.7	25.0	-	3.6
	Combined	43	11.6	48.9	20.9	18.6	-	3.5
Sturgeon Bay June 27	Male	82	8.5	67.1	22.0	2.4	-	3.2
	Female	71	1.4	38.0	47.9	12.7	-	3.7
	Combined	153	5.2	53.6	34.0	7.2	-	3.4
Unweighted mean all ports	Male	-	8.6	59.9	26.8	4.7	-	3.3
	Female	-	2.7	41.1	41.0	14.8	0.4	3.7
	Combined	-	5.5	50.2	33.9	10.2	0.2	3.5

at Saugatuck. The limited migration of age-II fish of the 1965 year class to the inshore areas, however, did not account entirely for their poor representation in the dieoff. As age-III fish in April 1968, the 1965 year class contributed only 16 percent of the adults in catches of experimental trawls at Saugatuck, whereas the average percentage contribution of the 1961-64 year classes at age III in earlier collections was 41 percent.

Age-groups III and IV were the principal age groups of adults in the dieoff samples and in the bottom trawl collections. The higher percentages of age-III fish in the dieoff than in the trawl samples may reflect a later inshore movement of younger fish that were not vulnerable earlier to trawls.

The two oldest age groups of alewives (VI and VII) were poorly represented in all collections, but were less numerous

Table 3. Age composition (percentage) by sex of adult alewives taken in experimental trawls at four locations in Lake Michigan April and June 1967

Location and date	Sex	Number of fish	Age group						Average age
			II	III	IV	V	VI	VII	
Benton Harbor April 19	Male	41	-	53.7	41.5	4.8	-	-	3.5
	Female	65	3.1	32.3	55.4	9.2	-	-	3.7
	Combined	106	1.9	40.6	50.0	7.5	-	-	3.6
Saugatuck April 13	Male	71	5.6	45.1	43.7	5.6	-	-	3.5
	Female	74	-	27.0	60.8	12.2	-	-	3.9
	Combined	145	2.8	35.8	52.4	9.0	-	-	3.7
Frankfort June 11	Male	62	3.2	51.6	40.3	3.2	1.6	-	3.5
	Female	82	1.2	11.0	64.6	19.5	2.4	1.2	4.1
	Combined	144	2.0	28.5	54.2	12.5	2.1	0.7	3.9
Sturgeon Bay[1] June 9	Male	99	13.1	60.6	26.3	-	-	-	3.1
	Female	115	8.7	43.5	41.7	5.2	-	0.9	3.5
	Combined	214	10.7	51.4	34.6	2.8	-	0.5	3.3
Average all ports	Male	-	5.5	52.8	37.9	3.4	0.4	-	3.4
	Female	-	3.3	28.5	55.6	11.5	0.6	0.5	3.8
	Combined	-	4.3	39.1	47.8	8.0	0.5	0.3	3.6

[1] Lake Michigan off Sturgeon Bay Canal.

in the dieoff samples than in the trawl collections. The percentage of VI-group fish was 0.2 percent in the dieoff samples and 0.5 percent in the trawl collections. Age-VII fish appeared in only two of the trawl collections (0.3 percent) and were absent in the dieoff alewives. Older fish in the trawl samples may have died before late June when most of the collections were made from the dieoff. A decrease in the ages of spawning-run alewives at Chicago in 1966 between late April and early June (data unpublished) suggests that older fish spawn earlier and many may die during the early weeks of the spawning season.

Average Lengths of the Age Groups

The mean lengths of alewives of age-groups II-V in the samples from the dieoff were either smaller than or identical to those in the trawl collections (Tables 4 and 5).

The average lengths of alewives are presented separately by sex because of sex differences in growth rate that begin in the third year of life. In all collections the average lengths

Table 4. Average lengths (mm) of male and female alewives at various ages in the dieoff samples from six locations in Lake Michigan and Sturgeon Bay, June 1967

[Number of fish in parentheses]

Location and date	Sex	Age group II	III	IV	V	VI	All ages
Michigan City June 28-29	Male	147	155	165	170	–	159
		(2)	(45)	(29)	(3)		(79)
	Female	142	157	173	179	–	165
		(1)	(36)	(33)	(5)		(75)
	Combined	145	156	169	176	–	162
		(3)	(81)	(62)	(8)		(154)
St. Joseph June 29	Male	146	154	169	179	–	158
		(4)	(50)	(17)	(4)		(75)
	Female	–	160	171	181	–	168
			(22)	(25)	(7)		(54)
	Combined	146	156	170	180	–	162
		(4)	(72)	(42)	(11)		(129)
Saugatuck June 29	Male	134	154	168	180	–	157
		(6)	(23)	(13)	(2)		(44)
	Female	132	158	173	182	–	167
		(1)	(23)	(26)	(6)		(56)
	Combined	134	156	171	181	–	162
		(7)	(46)	(39)	(8)		(100)
Ludington June 28	Male	144	153	164	167	–	155
		(3)	(38)	(13)	(1)		(55)
	Female	135	158	170	177	187	167
		(3)	(25)	(39)	(18)	(1)	(86)
	Combined	140	155	168	176	187	162
		(6)	(63)	(52)	(19)	(1)	(141)
Frankfort June 9	Male	135	143	161	160	–	148
		(3)	(9)	(5)	(2)		(19)
	Female	137	152	168	180	–	160
		(2)	(12)	(4)	(6)		(24)
	Combined	136	148	164	175	–	155
		(5)	(21)	(9)	(8)		(43)
Sturgeon Bay June 27	Male	135	152	166	164	–	154
		(7)	(55)	(18)	(2)		(82)
	Female	132	154	166	180	–	163
		(1)	(27)	(34)	(9)		(71)
	Combined	135	153	166	177	–	158
		(8)	(82)	(52)	(11)		(153)
Unweighted mean all ports	Male	140	152	166	170	–	155
	Female	136	157	170	180	187	165
	Combined	139	154	168	178	187	160

Table 5. Average lengths (mm) of male and female alewives at various ages in trawl samples from four locations[1] in Lake Michigan, June and April 1967

[Number of fish in parentheses]

Location and date	Sex	Age group						All ages
		II	III	IV	IV	VI	VII	
Benton Harbor April 19	Male	-	158 (22)	165 (17)	177 (2)	-	-	162 (41)
	Female	142 (2)	157 (21)	170 (36)	182 (6)	-	-	166 (65)
	Combined	142 (2)	157 (43)	169 (53)	181 (8)	-	-	165 (106)
Saugatuck April 13	Male	144 (4)	159 (32)	168 (31)	173 (4)	-	-	163 (71)
	Female	-	164 (20)	175 (45)	188 (9)	-	-	174 (74)
	Combined	144 (4)	161 (52)	172 (76)	184 (13)	-	-	168 (145)
Frankfort June 11	Male	140 (2)	157 (32)	167 (25)	174 (2)	187 (1)	-	162 (62)
	Female	137 (1)	161 (9)	173 (53)	180 (16)	200 (2)	172 (1)	173 (82)
	Combined	139 (3)	158 (41)	171 (78)	179 (18)	195 (3)	172 (1)	168 (144)
Sturgeon Bay[2] June 9	Male	140 (13)	154 (60)	165 (26)	-	-	-	155 (99)
	Female	136 (10)	154 (50)	172 (48)	185 (6)	-	215 (1)	162 (115)
	Combined	138 (23)	154 (110)	170 (74)	185 (6)	-	215 (1)	159 (214)
Unweighted mean all ports	Male	141	157	166	175	187	-	160
	Female	138	159	172	184	200	194	169
	Combined	141	158	170	182	195	194	165

[1] Fish from Grand Haven were not aged.

[2] Lake Michigan off Sturgeon Bay Canal.

of the females exceeded those of the males by 2-3 mm at age III and 9-10 mm at age V. Age-III, -IV, and -V females were longer than males in 27 of 30 comparisons. Age-II females were slightly smaller than II-group males but the difference does not reflect slower growth for females because second-year calculated lengths of the sexes of older fish are identical. More large age-II males than females apparently mingle with the adult population.

Faster growth of the female alewife in Lake Michigan was noted by Joeris and Karvelis[3] for fish from commercial pound nets in Green Bay and recently by Norden (1967) who reported an average difference of 4 mm between the sexes in a pooled sample of age-I, -II, and -III fish.

Sex Composition

The sexes were nearly equally represented in the samples of alewives from the dieoff. The percentage of females for all ages combined, exclusive of age I for which sex could not be determined, ranged from 42 percent at St. Joseph to 61 percent at Ludington and averaged 52 percent for the six locations (Table 6).

The percentage of females was slightly higher in the trawl samples (56 percent), but changes in sex composition with increases in age were similar in most collections (Table 6 and 7). The consistent change in sex composition was marked by more males than females at ages II and III and more females than males at ages IV through VII in all the collections except the small sample of age-IV fish from the dieoff alewives at Frankfort.

Condition of the Body

Alewives in the dieoff were generally robust despite the presence of hemorrhaging and fungus on some fish. Emaciated fish, common in bottom trawl catches in late July and August when the condition of adults is normally the poorest, were not conspicuous in the dieoff. The normal condition of the body was confirmed by weight comparisons between alewives in the dieoff at St. Joseph and Michigan City and those from the spawning migration at Chicago, May 26-June 13, 1966 (Table 8). Unweighted means of the body weights of males and females in length groups from 130-139 to 180-189 mm

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[3] Joeris, Leonard S., and Ernest Karvelis. 1962. The present status of our knowledge of the biology of the alewife in northwestern Lake Michigan and Green Bay. U. S. Bureau of Commercial Fisheries, Ann Arbor Biological Laboratory. File report 6 p. (typewritten).

Table 6. Percentage of females in different age groups[1] of alewives in the dieoff samples from six locations in Lake Michigan and Sturgeon Bay, June 1967

[Number of fish in parentheses]

Location and date	Age group					All ages
	II	III	IV	V	VI	
Michigan City June 28-29	33 (3)	44 (81)	53 (62)	62 (8)	-	49 (154)
St. Joseph June 29	0 (4)	31 (72)	60 (42)	64 (11)	-	42 (129)
Saugatuck June 29	14 (7)	50 (46)	67 (39)	75 (8)	-	56 (100)
Ludington June 28	50 (6)	40 (63)	75 (52)	95 (19)	100 (1)	61 (141)
Frankfort June 9	40 (5)	57 (21)	44 (9)	75 (8)	-	56 (43)
Sturgeon Bay June 27	12 (8)	33 (82)	65 (52)	82 (11)	-	46 (153)
Unweighted mean all ports	25	42	61	76	100	52

[1] Exclusive of age I.

were 25.5 and 26.7 grams, respectively, in the dieoff and 25.9 and 26.6 grams in the spawning run at Chicago. Males are lighter than females at all times of the year in Lake Michigan.

Condition of the Gonads

The presence of many immature yearling alewives and unspawned adults in the dieoff is proof that spawning attrition was not the major cause of the dieoff. Large percentages (32-67) of marine alewives die after spawning in freshwater streams (Cooper, Havey, 1961) and spawning mortality undoubtedly occurs annually in Lake Michigan, but nonetheless more than 80 percent of the dead or dying fish (exclusive of

Table 7. Percentage of females in different age groups[1] of alewives in the trawl samples from four locations in Lake Michigan, April and June 1967

[Number of fish in parentheses]

Location and date	Age group						All ages
	II	III	IV	V	VI	VII	
Benton Harbor April 19	100 (2)	49 (43)	68 (53)	75 (8)	-	-	61 (106)
Saugatuck April 13	0 (4)	38 (52)	59 (76)	69 (13)	-	-	51 (145)
Frankfort June 11	33 (3)	22 (41)	68 (78)	89 (18)	67 (3)	100 (1)	57 (144)
Sturgeon Bay[2] June 9	43 (23)	45 (110)	65 (74)	100 (6)	-	100 (1)	54 (214)
Unweighted mean all ports	39	38	65	83	67	100	56

[1] Exclusive of age I.

[2] Lake Michigan off Sturgeon Bay Canal.

yearlings) from Saugatuck, Ludington, and Sturgeon Bay were either in prespawning condition or immature (Table 9).

The actual developmental stage of fish classified as "may spawn" in Table 9 does not weaken this conclusion because they definitely had not spawned before the dieoff. Lack of a sharp difference between partly spent and spent males, however, may have caused some misclassifications in the "will spawn" and "spent" categories.

Stomach Contents

Of 100 stomachs examined from adult alewives in the dieoff at Michigan City and St. Joseph, only 50 percent contained food (mostly small quantities of zooplankton). The small amounts of food and the empty stomachs were not unusual because alewives normally do not feed for extended periods before and during spawning (Cooper, 1961). Presence of the rapidly digestible zooplankton indicates that many fish were feeding just before death.

Table 8. Average weight (grams) of alewives from the dieoff at St. Joseph and Michigan City, June 28-29, 1967, and from the Chicago Central District Filtration Plant, May 26 and June 13, 1966

[Number of fish in parentheses]

Total length (millimeters)	Males		Females	
	1966 Chicago	1967 dieoff	1966 Chicago	1967 dieoff
120-129	18 (1)	13.0 (3)	-	-
130-139	16.7 (3)	17.2 (11)	15.3 (3)	17 (1)
140-149	20.6 (11)	20.8 (32)	22.8 (5)	21.5 (16)
150-159	23.4 (37)	23.4 (72)	24.5 (16)	24.4 (34)
160-169	27.4 (67)	27.4 (67)	28.7 (48)	28.7 (56)
170-179	31.2 (39)	29.9 (25)	31.3 (50)	32.9 (47)
180-189	36.0 (16)	34.5 (2)	36.8 (23)	35.7 (13)
190-199	40.0 (2)	-	40.6 (5)	51 (1)
200-209	-	-	47.7 (3)	-
Unweighted mean[1]	25.9	25.5	26.6	26.7

[1] Over length intervals of 130 through 189 mm.

Fungus Infection and Subcutaneous Hemorrhaging

Substantial numbers of dying alewives at the various sample locations were infected by *Saprolegnia*, were hemorrhaging subcutaneously, or were both infected and hemorrhaging. The possible significance of these conditions was investigated from their occurrence among fish in the selected samples from the dieoff at Michigan City and St. Joseph.

Saprolegnia is common in freshwater where it often engulfs the fertilized eggs of fish and invades the body surfaces of adults that are damaged in the act of spawning (Webster, 1948; Davis, 1953; Brown, 1960). Floating alewives that have

Table 9. Condition of the gonads of alewives in the dieoff collections from Saugatuck, Ludington, and Sturgeon Bay, June 27-29, 1967

[Age-group I excluded]

Total length (millimeters)	Number of fish							
	Immature		May spawn[1]		Will spawn[2]		Spent	
	Male	Female	Male	Female	Male	Female	Male	Female
120-129	-	-	2	1	-	-	-	-
130-139	1	3	4	-	6	1	-	-
140-149	1	-	6	5	12	9	5	-
150-159	-	1	13	4	17	12	7	4
160-169	-	-	9	13	14	24	10	9
170-179	-	1	4	9	4	41	2	8
180-189	-	-	1	2	1	16	-	8
190-199	-	-	-	1	-	2	-	2
Total	2	5	39	35	54	105	24	31
Percentage	2	3	33	20	45	59	20	18

[1] Condition intermediate between adjacent categories.

[2] Gonad in advanced state, ripening, or ripe.

been dead for long periods are usually matted with the fungus which Graham (1956) observed on the bodies of two alewives in a school that suddenly began to surface and die in one of the Lake Ontario mortalities.

Twenty percent of the alewives from the samples at Michigan City and St. Joseph were infected by the fungus which formed dense, isolated patches on some fish and was broadly dispersed on others (Table 10). The greater rate of infection for females than males (26 percent for females; 13 percent for males) was statistically significant ($X^2 = 4.349$; 1 d.f.; $p<0.05$), but length frequencies of the infected fish of both sexes did not differ significantly from the frequencies expected under the hypothesis of a common infection rate for all size groups:

Sex	d.f.	X^2	p
Male	3	1.167	>0.75
Female	4	6.458	>0.10

Because of its low incidence, *Saprolegnia* was not an important factor in the dieoff although infected fish were probably

Table 10. Incidence of fungus infection and subcutaneous hemorrhages among dying alewives, Michigan City, Indiana, and St. Joseph, Michigan, June 28-29, 1967

Total length (millimeters)	Total number of fish		Number of fish with: No fungus or hemorrhage		Fungus		Hemorrhage	
	Male	Female	Male	Female	Male	Female	Male	Female
130-139	4	-	2	-	1	-	2	-
140-149	17	11	9	5	1	1	8	5
150-159	48	15	23	4	8	6	24	6
160-169	42	32	14	17	6	9	24	12
170-179	13	28	5	14	1	4	7	11
180-189	2	6	1	1	-	4	1	4
190-199	-	1	-	1	-	-	-	-
Total	126	93	54	42	17	24	66	38
Percentage of total	100	100	43	45	13	26	52	41
Average length	158	165	157	166	157	166	159	166

more vulnerable to conditions causing death than were uninfected fish.

Hemorrhaging that produced fresh blood streaks along the lines of scale imbrication and denser blotches on some individuals was present on a much higher percentage of the dying alewives (47 percent) than was fungus infection (Table 10). A higher incidence among the males was not statistically significant ($X^2 = 1.513$; 1 d.f.; $p > 0.10$), nor did the length frequencies of the hemorrhaged fish differ significantly from the frequencies expected if the condition had been randomly distributed among the length groups:

Sex	d.f.	X^2	p
Male	5	0.385	>0.995
Female	4	0.581	>0.95

Because the hemorrhages were fresh and well distributed among all sizes of both sexes of the dying alewives, they may have been a symptom or physiological response to the cause or causes of the dieoff. Even if the hemorrhaging was coincidental, however, it may have increased vulnerability to the actual cause of death. Any hemorrhaged fish that escaped immediate death would have been susceptible to *Saprolegnia* which rapidly infects wounded and weakened individuals (Davis, 1953).

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Pesticides in the Estuary

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Pesticides in the Estuary[*] [†]

ABSTRACT

Organochloride pesticides contaminate the major drainage basins in the United States. Examples are given of how and when this pollution occurs, its effect on estuarine fauna, and its eventual dispersal.

There are several pre-Christian references to the use of chemicals for the control of pests, but the first large-scale application of a pesticide was made only 100 years ago. In 1867, Paris Green was used successfully in the Rocky Mountain area for the control of a massive invasion by the potato beetle. The use of pesticides has accelerated since then to the extent that in 1966 more than $1 billion worth was sold throughout the world and it has been predicted that this amount will double in the next decade.

Present estimates are that about 100 million acres of the conterminous United States are sprayed or treated in some way each year with one or more pesticides compounds. In addition, more than one-third of our urban population lives near, and dumps its waste products into, estuarine drainage systems. So, the fact that we have pesticides in our estuaries is no surprise.

Pesticides are well-regulated chemicals and, with a few outstanding exceptions, significant levels of pollution resulting from them are derived from approved uses for the control of specific pests. We are observers of this pollution in the estuary but, at present, are in no position to control or manage chemical contamination which comes primarily from distant and unknown sources. This report does not consider pesticide pollution resulting from careless or accidental applications.

HOW PESTICIDES GET INTO THE ESTUARY

About 2 million acres of salt-water marsh and tidelands are treated annually to control noxious insects such as flies, gnats, and mosquitoes. Even when correctly handled, these applications may cause minor losses of fish and shellfish. We are willing to accept these losses, however, for the sake of our personal comfort. Formerly, DDT in oil or emulsion formulations was the preferred pesticide because it appeared to cause little damage to beneficial organisms at concentrations required to control insects. As we learned more about its persistence and magnification in the food web, however, other pesticides,—especially the organophosphates—were substituted because of their relatively faster rate of decay.

Minor applications of pesticides have been made directly in the

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[†] Contribution No. 85.

estuary on an experimental basis, primarily to control estuarine pests of oyster populations. Predation on oysters by at least four species of boring snails or drills, and the destruction of suitable oyster bottoms by burrowing shrimps cause incalculable financial losses wherever oysters are cultivated. To control these and other pests, chlorinated benzenes, lindane, DDT, and carbamates, alone and in combination, have been applied directly to mud flats, sprayed on the water surface, and incorporated into baits. These experiments have been unsuccessful for the most part, not only because of the damage to non-target animals but also because of their failure to eliminate the problem species. I am confident, however, that the search will go on to find specific chemical or biological controls for these pests because of their great economic importance.

Municipal and industrial wastes transport significant but essentially unknown amounts of pesticides into drainage basins annually. These sources are perhaps the most amenable to control today, but from the standpoint of know-how rather than cost. The effects of this pesticide pollution are usually obscured by the sheer volume or toxicity of other waste products in the effluent. There have been notable instances, however, of long stretches of rivers and estuaries that were contaminated by pesticide manufacturers whose effluents consisted largely of mixtures of pesticide chemical by-products.

Pesticides reach the estuarine environment indirectly and to some unknown extent through the agency of atmospheric drift and precipitation. The loss of DDT and other pesticides to the atmosphere by means of co-distillation and wind currents during forest spray operations is well documented.

I recall an incident that occurred several years ago during an experimental spraying of Alaskan forests to control spruce budworm, a defoliating caterpillar of considerable economic importance. I observed the progress of the operation from a helicopter about one thousand feet above the spray plane. At this level, the odor of the fuel oil in which the DDT was dissolved was clearly detectable. It was estimated then that perhaps one-third of the DDT failed to contact the target area because of air currents, despite the fact that spraying was done in the early morning when wind velocity was at a minimum. This aerially dispersed DDT can appear later in the form of rain and contaminate watersheds far from the spray area.

During this particular experiment, pre-spray examination of endemic fish in forest streams revealed DDT-DDE residues as high as 0.8 ppm. Presumably, this area had not been exposed to pesticides for 20 years. Recent studies have shown that DDT sprayed incidentally on forest streams has caused the death of aquatic insects at least 30 miles downstream from the spray area. This mortality may result in the starvation of fish that survived the pesticide itself.

Of greater importance than the incidental spraying of forest streams is the fact that a majority of the aerosol droplets—up to 95 percent of the portion that falls to earth—fails to contact the target organisms but contaminates the forest canopy and ground.

Persistent pesticides may be leached eventually into surface waters and carried on silt through the drainage basin. To increase the efficiency of such aerosols, special equipment disperses them into even smaller, more penetrating droplets, but this improvement may be self-defeating since the smaller droplets are more responsive to air currents and a larger proportion may drift away from the target area.

The largest contribution of pesticides to the estuary is derived from their registered use on orchards and farm lands.

Clay, silt, and detritus sorb the particles of insoluble, persistent pesticides and, depending on the degree of erosion, more or less of the chemical is carried away in surface waters. It has been estimated that as many as 11 tons of soil per acre may be washed away in a year where farming practices are poor. This is the extreme of bad usage; under the best conditions, none is lost. We realize that between these extremes an alarming amount of soil with its accompanying pesticides burden is washed downstream and into the estuary each year. The evidence for this transport of pesticides appears in the pesticide monitoring program which the Bureau of Commercial Fisheries has been conducting for the past several years.

WHEN PESTICIDES APPEAR IN THE ESTUARY

The pesticide monitoring program is cooperative with state conservation agencies, university-affiliated marine laboratories, and other federal laboratories in 14 states on the Pacific, Atlantic, and Gulf coasts. About 175 permanent stations are in estuaries having shellfish populations. Samples of any one of nine species of clams, oysters or mussels, depending on the estuary, are collected at 30-day intervals and analyzed for residues of 10 of the more common organochloride pesticides.

We find that levels of pesticide residues in these mollusks reflect the agricultural practices of the particular drainage basin. The drainage basin of Wallapa Bay, Washington, for example, is small and consists primarily of forested slopes; there is little agriculture. DDT residues in oysters are as low as we find anywhere in the nation—20 ppb or less—and typically occur only during the first half of the year.

Oysters from the Rappahannock River in Virginia contain DDT residues throughout the year but a seasonal peak during the spring, indicates the farmland nature of this drainage basin. A similar spring peak appears in the adjacent James River, but residues are at a much higher level throughout the year. We attribute this continuously higher level to the large volume of industrial and municipal wastes that are discharged regularly into this river basin.

In contrast to these estuaries, the Arroyo Colorado on the southern coast of Texas presents a unique situation. This basin drains a rich area of truck farms and cotton and citrus land. Much of the area is harvested three times a year, and nearly 18 pounds of pesticides are applied per acre per year. As a result, we find three seasonal peaks in residues in the shellfish, and total amounts present (up to 0.5 ppm) are higher than we routinely observe at any of the other monitor stations in the country.

The coincidence of peak loads of pesticide pollution and the spawning of many of the aquatic species in the spring endangers estuarine fauna in several ways. The developing gametes of most forms are a prime center for the deposition of chlorinated hydrocarbon pesticides because of the high metabolic activity and their lipid nature. We exposed oysters to 1.0 **part per billion** of DDT in flowing sea water for 12 days, for example, and analyses showed that the eggs accumulated 25 **parts per million** of DDT and its metabolites. We do not know the effect of this residue on oyster embryology but similar deposits in lake trout eggs caused almost complete reproductive failure. We find that young fish, and presumably other forms too, may be more tolerant of pesticides in the surrounding water than adults as long as they are nourished by their endogenous yolk. But when this yolk is exhausted, they start feeding on particulate matter in the plankton and become especially susceptible to pesticides carried by silt and plankton particles.

Juvenile animals, in general, are more susceptible than adults to pesticides, and peak populations of juveniles—both those hatched in the estuary and migrants from offshore waters—are present when pesticide pollution is usually highest, in the spring and early summer. This situation is of special concern to the commercial fishermen, since both shrimp and menhaden, respectively our most valuable and largest marine crops, migrate through the estuaries as juveniles.

THE CYCLING OF PESTICIDES IN THE ESTUARY

Pesticides entering the estuary on silt and detritus may become part of the bottom deposits, where they are taken up by bottom-dwelling worms and other benthic fauna. These animals, in turn, are eaten by crabs, fish, and other members of the food web. Recent studies in New York have demonstrated the accumulation of up to 32 pounds per acre of persistent pesticides in bottom deposits, where they may be available for years to bottom feeding animals or put into circulation by wave action. It is difficult to trace these relationships because we do not know the time the pesticides entered the estuary originally or the amount.

Pesticides applied directly to estuarine waters are immediately taken up by plankton. Recently we documented the accumulation of 8 ppm of DDT by oysters 24 hours after local beaches were sprayed to control stable flies. Plankton-feeding fish, such as mullet and pinfish, regularly accumulate pesticide residues which are passed on to predators, such as sharks and other fish, porpoise, and fish-eating birds. This biological magnification of residues in the food web may progress, for example, from an estimated 1.0 ppb in the water to 70 ppb in plankton to 15 ppm in fish and up to 800 ppm in porpoise blubber.

Residues in shrimp and other crustaceans are usually negligible or absent. I suspect that this is because they are more sensitive to insecticides than other estuarine fauna and are killed when exposed to this type of pollution, before they have opportunity to metabolize the poison.

HOW PESTICIDES LEAVE THE ESTUARY

We assume that a major portion of pesticide chemicals entering the estuary are lost through the processes of dilution, chemical decay, and fixation in bottom deposits. If the few specimens we have analyzed are typical, however, 10 mature porpoise immobilize approximately 1 pound of DDT and its metabolites in their bodies. Pinfish and Atlantic croaker populations in Pensacola Bay move offshore to spawn. When they do, they carry with them and lose in the spawning process each year about ½ pound of DDT accumulated in the estuary. We have no data on the effect of these DDT residues on pinfish and croaker progeny that develop in offshore waters, but evidence from other species suggests that embryo mortality may be increased significantly.

Other fish that spend part of their life span in the estuaries, such as menhaden and sardines, move offshore where they are preyed on by pelagic tuna and similar oceanic fish. As a result, tuna populations in the mid-Pacific and South Atlantic contain significant levels of pesticide residues which they transport to all parts of the world oceans. Relatively large amounts of pesticides are accumulated by fish-eating birds is estuaries, which then distribute them along their migratory pathways.

In summation, I feel that pesticides are causing significant changes now in estuaries that are only moderately polluted. The interaction of the many physical and biological factors makes the net effect unpredictable at this time. Despite the fact that the pollution load does not now constitute a human health hazard, the evidence is clear that changes from pesticides may have long-lasting deleterious effects on marine productivity and the world food supply.

We must reject, out-of-hand, the increasingly voiced hypothesis that pesticides as we know them are essential to the world economy. The enormous benefits that have accrued through their use make mandatory our search for new, equally beneficial but selectively toxic materials and management methods which will not degrade the estuarine environment.

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PESTICIDE RESIDUES IN ESTUARINE MOLLUSKS

Philip A. Butler [1]

The release of DDT for civilian use after World War II resulted in its widespread application to coastal marshes for the control of mosquitoes and other pests. Inevitably, misuses caused some identifiable wildlife losses in localized areas. Reported increased mortality in fish and crab populations aroused the concern of many biologists and fishermen, but it was not until 1958 that research funds were made available to the Bureau of Commercial Fisheries to study this growing problem.

Although most of the species of crustaceans, fish, and shellfish that make up our commercial harvest from the sea are dependent on the estuarine environment during some period of their life cycle, the amount of pesticide pollution in estuaries and its effect on the biota were essentially unknown when the research was initiated.

One of the first requirements of the program was to develop objective techniques for measuring the toxic effects of pesticides. It is relatively simple to determine the pollution levels that will cause acute toxic reactions -- for example, the amount of a pesticide required to kill a particular species of animal in a given period of time. It is much more difficult and (we realize now) much more important to determine the consequences of chronic low levels of pollution. A toxicant in the environment at sublethal concentrations might interfere with growth or reproduction without ever being noticed or, at least, identified as the causal agent.

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The large body of knowledge about the physiology of oysters and their sensitivity to trace elements in the estuarine habitat suggested their use as biological indicators of pesticide pollution in the environment. Laboratory evaluation showed that oysters were, in fact, extremely sensitive to trace amounts of pesticides as well. Oysters stopped feeding and exhibited erratic shell movements during experimental exposures to less than 1 part per million of many of the organochloride pesticides.

Additional testing revealed that the metabolic processes involved in the formation of shell are inhibited by some pesticides at levels as low as a few parts per billion. This reaction has now been used for a standard bioassay test. After the valve edges of small, rapidly growing oysters are ground uniformly smooth, 12 oysters are exposed in flowing sea water aquaria to each of three or more serial dilutions of the test chemical. The amount of shell deposited in 96 hours by control oysters in unpolluted water -- up to 3/8 inch -- is used as a standard to calculate the chemical's toxicity. In general, the relation of shell deposition to toxicant concentration is logarithmic.

Interference with shell deposition is evidence of an acute toxic effect on the oyster, but it is apparent only at concentrations higher than would usually be expected in polluted estuaries. It was necessary to determine whether the oyster is affected in some more subtle way by still lower levels of pesticide pollution. Because oysters are known to extract and store in their tissues copper and other metals present in trace quantities in sea water, the appropriate exposure tests and chemical analyses were conducted to determine whether the oyster responded in a similar way to low concentrations of pesticides.

Data from several tests are tabulated in Table 1 to show the degree of concentration or biological magnification of DDT in oysters after they were exposed to flowing sea water experimentally contaminated with the pesticide.

The inverse relationship between the biological concentration factor and the amount of DDT in the water suggests that as the environmental concentration of DDT increased it interfered chemically to an increasing extent with the metabolism of the oyster. Alternatively, increasing concentrations of DDT may inhibit the oyster's feeding and indirectly lower the rate of biological magnification.

Stored DDT is flushed from oysters gradually when they are transferred to unpolluted water. DDT residues of 150 ppm may require 3 months or longer, depending on water temperatures, to disappear from oyster tissues. Residues of less than 0.1 ppm are usually lost in about 2 weeks.

Since these laboratory data on residues needed field corroboration, a project was established to monitor DDT residues in an oyster population near Gulf Breeze. Duplicate samples were collected and analyzed monthly.

Analysis of a composite sample of as few as 12 oysters is sufficient to produce a reliable index of average residue levels in an oyster population. The oysters from this local population nearly always had a 'background' residue of DDT and its metabolites ranging from 10 ppb -- the lower limit of sensitivity of our analytical procedures -- to about 70 ppb. Occasional analyses indicated residues as high as 8 ppm that were the result of the direct applications of DDT to the aquatic environment in vector control programs.

During the first 2 years of this monitor project, the correlation was good between peak residues in oysters, high river stages, and the season of maximum agricultural use of pesticides in the drainage basin. Correlation was excellent between increased residues in oysters and the timing of local projects in which DDT was sprayed along the beaches for stable fly control. DDT residues increased a thousandfold in both plankton and oysters collected from areas near sprayed beaches.

It became apparent that the periodic monitoring of oyster populations would provide a sensitive index of the degree of organochloride pesticide pollution in an estuary, the time the pollution appeared, and how long it persisted.

The utility of oysters as biological monitors is due not only to their sensitivity to the pesticide, but also to their ability to gain and lose residues depending on the level of pollution, their fixed position in relation to the flow of water, their ubiquity, and the ease with which they can be sampled or transplanted.

Laboratory and field evaluations show that fish would be much less useful as biological monitors. Not only do fish migrate unpredictably and feed selectively, but pesticide residues in fish increase with time and are not lost as the environmental pollution abates. Fish and other vertebrates store pesticides primarily in localized fat depots. These residues are then metabolized and lost when fat stores are mobilized during periods of starvation or gamete formation. As a result, it is nearly impossible to interpret the significance of pesticide residues in fish. They may accumulate slowly over a long period directly from the surrounding waters, or rather rapidly, as a result of a contaminated dietary component. A residue may represent the peak accumulation or some unknown lesser percentage. Individual fish from the same school and year class may differ widely in the total amount of accumulated pesticide; sample size must be increased accordingly to minimize the effect of these differences.

Numerous laboratory experiments were conducted to gain some understanding of the biological significance of pesticide residues in field samples. Oysters were exposed to DDT in different experiments until they contained body residues ranging from 2 to 4 ppm. These and higher levels of DDT had been observed in our field samples from time to time. The oysters were then fed to laboratory populations of commercial species of shrimp and fish. In all tests, the mortality of the test animals was low; one or two individuals died daily. The longer the experiment lasted, however, the greater was the cumulative mortality. At the end of 2 to 4 weeks, at least 50 percent of the experimental animals had died. Deaths in control populations were negligible. It would be impossible to detect such small daily losses under field conditions.

The experiments were faulty in that the contaminated oysters made up the entire diet of the test animals; this condition would be unlikely in nature. Nevertheless, the results suggest that low levels of pesticide pollution in the estuarine environment could be responsible for significant but unidentified increases in the mortality of both commercial and non-commercial species.

Knowledge of the geographical extent and magnitude of pesticide pollution in estuaries is essential for an understanding of the seriousness of the problem. Therefore, a nationwide program was initiated in 1965 to monitor periodically shellfish populations in coastal estuaries. The success of this program has been due in large part to the widespread interest in its objectives. Fourteen state, university, and federal laboratories cooperate in collecting and processing the samples. All of the samples are sent to the laboratory in Gulf Breeze for analysis to eliminate inter-laboratory variations in methodology.

This laboratory has developed a method of homogenizing the biological samples with sodium sulfate and precipitated silica which prevents pesticide residues from decaying at room temperatures. This makes possible the mailing of unrefrigerated samples across the country, and has facilitated greatly the handling of large numbers of samples.

Repetitive sampling at some monitor stations soon demonstrated that significant amounts of pesticides were consistently present in oyster samples although the pollution source was unknown. To pinpoint the origin of the pollution, trays of oysters were placed successively closer to the head of the estuary; but these also built up high residues. Above this region the water was too fresh for oysters, and, to continue the search, a brackish or fresh water mollusk had to be substituted for oysters.

A similar situation exists in some estuaries which, although saline enough to support oyster populations, have (for one reason or another) only clam or mussel populations in sufficient abundance to be routinely monitored over a period of years. It became necessary, therefore, to determine the relative significance of assay data obtained under controlled conditions when different species of mollusks were used as indicator organisms.

Under similar test conditions the soft clam, *Mya arenaria*, proved to be the most sensitive or efficient in storing organochloride residues. The other bioassay animals tested, in order of decreasing sensitivity, were: the eastern oyster, *Crassostrea virginica*; the brackish water marsh clam, *Rangia cuneata*; the fresh water Asiatic clam, *Corbicula manillensis*; and the quahog or hard clam, *Mercenaria mercenaria*. These relationships, together with the rate of loss of residues when the animals were held in clean flowing sea water for 7 days, are tabulated in Table 2.

The actual residue levels vary, depending on the hydrographic conditions of the experiment and the metabolic activity of the test animals. The relative efficiency of the test species probably reflects the rate of water transport through the gills in relation to the mass of the animal.

Another test animal that has not been evaluated fully is the mussel, several species of which appear to equal the eastern oyster in sensitivity. On the Pacific coast, both the introduced Pacific oyster, Crassostrea gigas, and the native oyster, Ostrea lurida, which are routinely monitored in some areas, do not appear to be as efficient as the eastern oyster.

Laboratory tests show, too, that the organochloride pesticides are not all taken up at the same rate by the same test species, nor does the sensitivity of the different test species always vary in the same relative order. It is fortunate for monitoring purposes that DDT, the most persistent and widely used pesticide, is also concentrated most readily by all of the test species. Lindane is at the opposite end of the scale, and the other organochlors tested are arrayed in unpredictable order between those two (Table 3).

The monitor program now has about 160 permanent stations in estuaries with shellfish populations. Samples of any one of nine species of clams, mussels, or oysters -- depending on the estuary -- are monitored at 30-day intervals. About 6,000 duplicate samples have been collected and more than 4,000 analyses performed during the past 2 years. Gas-liquid chromatography with electron capture analytical techniques are used with two columns of different polarity so that the following compounds are clearly resolved and can be quantified: aldrin, BHC, dieldrin, DDT, TDE, DDD, endrin, heptachlor, heptachlor epoxide, lindane, and methoxychlor. In samples from areas of special interest we search occasionally for toxaphene and Mirex. Identified compounds are quantified at levels above 10 ppb; when necessary, identifications are confirmed with thin-layer chromatographic techniques.

The monitor program is demonstrating the widespread occurrence of estuarine pollution due to the organochloride pesticides. Tissue residues of DDT and its metabolites in mollusks are, for the most part, less than 0.1 ppm. In only one estuary are residues typically as high as 0.1 to 0.5 ppm, and in many others the pesticide residues are absent for 6 or more months of the year. Concentrations of residues follow a seasonal pattern and are usually highest in early summer. This peak is to be expected if the residues are derived from surface waters draining agricultural land. In river basins supporting large urban populations, pesticide residues are consistently high throughout the year, although seasonal peaks may still be detected.

In one area in south Texas, intensive truck farming produces three crops annually. At least six different pesticides are applied to one or more of the major crops in this river basin and a total of about 18 pounds are applied per acre per year (Table 4). These practices are reflected in the three seasonal peaks and the generally high levels of pesticide residues in monitoring samples. Average residue levels are about five times higher than in samples from other agricultural areas. Biologists are investigating now the possibility of a causal relationship between this heavy pesticide load and the reproductive failure in a local population of a commercially important species of estuarine fish.

Monitor samples from river basins in the state of Washington show the least evidence of pollution throughout the year, and, conversely, samples from the Gulf of Mexico littoral, which receives the drainage from half of the United States, are always contaminated to some extent.

On the basis of laboratory experiments, pesticide residues observed in monitor samples from most areas appear to indicate concentrations of water-borne pesticides that are too small at any one time to cause detectable damage to the biota. The danger in this pollution lies in the fact that persistent pesticides are concentrated, cycled, and magnified in the food-web. Small residues in the microscopic planktonic biota may be magnified a million times or more as they progress through small, then larger fish, and finally into top levels of the food web. Negligible pollution in estuarine water may have catastrophic effects eventually on porpoise, for example, and fish-eating birds.

The residues do not now appear to present a human health hazard. It must be remembered, however, that man is also at the top level of many food chains.

In summary, populations of sessile mollusks have distinct advantages as monitors of organochloride pollution in estuaries. Not the least of these are: sensitivity, ability to concentrate and lose residues, fixed position, and ease in handling. The described monitor program has shown that a majority of the estuaries in the United States are contaminated with organochloride pesticides, but not yet to the extent that they endanger man's food supply. The data have been useful in pinpointing sources of pesticide pollution and indicate areas in which we may expect to associate this type of pollution with declines in our commercial fishery resources.

Table 1. Uptake of DDT by the eastern oyster.

Length of exposure 7 to 15 days in different tests

Exposure concentration	Whole body residue	Biological magnification
ppb	ppm	x1000
10.0	150.0	15
1.0	30.0	30
0.1	7.0	70
0.01	0.72	70
0.0001	0.07	0
Control	0.06	

Table 2. Average uptake and loss of seven chlorinated pesticides by selected aquatic mollusks

Bioassay animal	Magnification in 5 days	Percent loss in 7 days
Soft clam	3000	90
Eastern oyster	1200	50
Marsh clam	700	50
Asiatic clam	600	30
Hard clam	500	75

Table 3. Range in magnification of chlorinated pesticides by five species of aquatic mollusks

Lindane	10 - 250x
Endrin	500 - 1250
Methoxychlor	300 - 1500
Dieldrin	700 - 1800
Heptachlor	250 - 2500
Aldrin	350 - 4500
DDT	1200 - 9000

Table 4. Recommended agricultural use of pesticides in the Laguna Madre area, Texas (average number of pounds per acre per year)

Pesticide	Cotton	Vegetables	Sorghum
DDT	3.5	6.0	
Dieldrin		1.6	
Endrin		1.6	
Parathion	1.0	1.4	1.0
Sevin	8.0	1.4	
Toxaphene	10.0	6.0	8.0
Total	22.5	18.0	9.0

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A RADIOGRAPHIC METHOD FOR DETERMINING GAS BLADDER VOLUME OF FISH.—Several methods have been used to estimate volume in the gas bladder of fish. Black (1948) removed the gas from the bladder of mummichog (*Fundulus heteroclitus*) underwater with a syringe and hypodermic needle and then allowed the gas to displace its volume in a calibrated bulb filled with water. Jones (1951) weighed perch (*Perca fluviatilis*) in a density bottle filled with water before and after the intact gas bladder was removed. The difference in weight times the density of water then equaled the amount of water displaced by the bladder and its enclosed gas. Alexander (1959a, 1959b, 1959c), working on a number of cypriniforms and other teleosts, and Brawn (1965), working on live pollock (*Pollachius virens*), measured changes in the volume of the gas bladder when the external pressure on either the excised bladder or the intact fish was experimentally varied. The original volume was then computed by Boyle's law. All these studies concerned fish that weighed no more than 0.2 kg.

An alternative method for estimation of gas bladder volume is presented here that can be easily used with large fish. Radiographs of the bladder *in situ* were taken and volume was computed from a geometrical reconstruction of the bladder, based on measurements of its dimensions in the radiographs. Cross sections of the gas bladder were assumed to be elliptical. The two ends of the bladder were assumed to be ellipsoidal cones. These estimates were checked by measuring the volume of water displaced by the gas in the excised bladder.

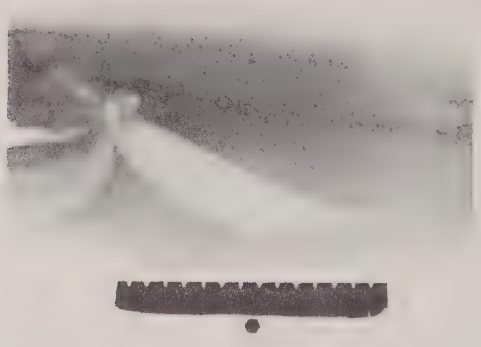

Fig. 1. Radiograph of a bigeye tuna, 54 cm fork length, showing view of gas bladder. Divisions of metal ruler = one cm.

Yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*T. obesus*) were caught (at the surface) near the Hawaiian Islands. The fish were placed in portable transfer tanks (Nakamura, 1966) and transported alive to shoreside facilities. On shore the fish were removed from the transfer tanks to die. Gas bladder measurements were completed within 45 min after death.

A Picker mobile X-ray unit with a 575 cathode tube transformer head was used with type 3000X Polaroid radiographic film to produce a positive print 23.7 by 27.1 cm. The film was 1.7 m beneath the X-ray projector. The equipment was set at 70 kw and 15 ma. Exposure times ranged from 0.25 to 4.0 sec, depending on the thickness of the fish. The 10-sec developing time of Polaroid film greatly facilitated the study because the radiographs could be immediately examined, and retaken if inferior.

Fish were radiographed from the dorsal and lateral views. For the dorsal view, the body was inclined with the head lower than the tail, so that the longest axis of the gas bladder was parallel to the film. This orientation of the fish was necessary because the longest axis of the gas bladder in the lateral view did not parallel the longitudinal axis of the fish (Fig. 1). The radiographs were calibrated with a metal ruler that was placed next to the fish at the approximate level of the gas bladder. The outline of the gas bladder was traced on paper from the film. Since the radiographs fade, the tracing was made soon after the print was dry.

Lengths of the vertical and horizontal axes of 4–18 elliptical cross sections along the length of the gas bladder were measured from the traced outlines of the gas bladder. Usually the gas bladder was shorter in one view than the other, either because its longest axis was not parallel to the film when the radiographs were taken or because the tip of the bladder was not clearly defined in the radiograph. When this difference occurred a geometrical method was used to match up the corresponding vertical and horizontal axes of each cross section in the two views. The vertical and horizontal axes of each elliptical cross section were then measured and the cross sections were treated as ellipses.

Volume between two cross sections was computed by multiplying the average area of the two ellipses by the distance between them. Volume between a cross section and the end of the gas bladder was computed by multiplying the cross section area and two-thirds of the distance between the cross section and the end of the gas bladder. In the bigeye tuna, two rounded protrusions occurred at the anterior end of the gas bladder (Fig. 1). Their volumes were computed by considering them as hemispheres. The volumes of all the geometrical units were then summed to give the estimate of volume within the gas bladder.

To evaluate the estimate, a displacement method was used as a check. Immediately after the radiographs were taken, the gas bladder was excised intact and immersed in a graduated cylinder for measurement of the volume of displaced water. The bladder was then punctured and the volume of water displaced by the tissue was measured. The difference between these volumes gave the volume of the gas. In six of 32 dissections the gas bladder broke and no estimate by displacement was obtained.

Before any of these gas bladder measurements were made, the fork length, mass in air, and volume of the intact fish were also determined for comparison with gas bladder volume. Fish volume was estimated by using Archimedes' principle to estimate the volume of water displaced by the intact fish. These data are not presented here.

The radiographic method gave dependable estimates. We estimated, by both radiography and displacement, the gas bladder volume of 11 yellowfin tuna, 44–82 cm fork length, and 15 bigeye tuna, 50–59 cm fork length.

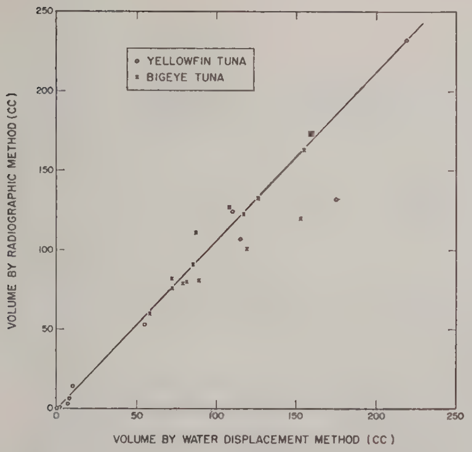

Fig. 2. Comparison between gas bladder volume estimated by a radiographic method and by a water displacement method.

The largest fish weighed 10 kg. When volumes from the radiographic method were plotted against the volumes from the displacement method (Fig. 2), the slope of the regression ($b = 1.085$) was not significantly different from 1 ($n = 26$, $t_{n-1} = 1.617$, $p > 0.10$), and the intercept ($a = -0.55$) was not significantly different from 0 ($n = 26$, $t_{n-2} = 0.0943$, $p > 0.10$). The correlation coefficient between the two sets of measurements was high ($r = 0.97$). It seemed unlikely that both methods had the same sources of error. Consequently, the similarity of the results lends credence to both methods.

The radiographic method described here has some unique advantages over other methods. The shape and position of the gas bladder are obtained without dissection. Samples are not lost by breakage during dissection. Mobile Polaroid X-ray units are simple to operate and can be used at sea or in the field. The ease and rapidity with which the Polaroid film is developed make it especially suitable for use at sea and by persons with little experience in estimating proper exposures. Although we did not make our measurements from live tuna, it seems likely that some species of fish could be anesthetized and radiographed alive in water —Bartlett and Haedrich (1966) demonstrated that fish could be effectively radiographed in water. We used the method only to estimate the volume within a large gas bladder, but it could also be used with more sophisticated equipment to determine volume of a small gas bladder.

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*Channelization and Spoiling in Gulf Coast & South Atlantic Estuaries** †

ABSTRACT

Channels and spoil banks are now a part of the estuarine environment. Several methods of construction are used that permit varying degrees of control over resulting spoil. Mechanical excavation with bucket dredges or draglines provides good spoil control on a small area. Hydraulic excavation, however, requires large spoil areas and affords poor control unless the spoil is removed from the construction site (hopper dredge) or retained within ring levees.

More than 200,000 acres of shallow coastal bays (not including marshes) in the Gulf and South Atlantic areas have been lost by dredging and filling over the past 20 years. In Texas alone, about 700 miles of Federal navigation channels have altered 13,000 acres of shallow bay bottoms and destroyed 7,000 acres of brackish marsh by deepening. Spoil from these channels has filled 55,000 acres of shallow bays and covered 23,000 acres of brackish marsh. It is not known how much estuarine habitat has been obliterated by private channels.

Other disadvantages of channelization and spoil dumping include segmentation of bays which promotes shoaling; increased saltwater intrusion; increased flushing time; altered tidal exchange, mixing, and circulation; increased turbidity; and loss of submerged aquatic vegetation. None of these changes, however, are as significant as the direct physical loss of habitat.

Advantages of channels and spoil deposition include connection of isolated waters and marshes to make them available as fish nursery areas, provision of routes of escape or refuge for fish during cold periods, improvement of water exchange and circulation, and release of nutrients trapped in bottom sediments.

Suggestions are given for planning channels and depositing spoil to reduce the loss of vital bay and marsh habitat. Research is needed so we can learn how to rehabilitate thousands of acres of barren spoil areas in our estuaries.

INTRODUCTION

Navigation channels are now part of the estuarine environment. Some estuaries have deep, wide channels capable of accommodating

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large ocean-going vessels; many have channels large enough to accommodate barge traffic; and others have only small channels for shallow-draft boats. Many estuaries have both large and small channels. Usually, the greater the population of people in the vicinity of an estuary the more numerous and larger the channels. I do not know of an estuarine system along the south Atlantic or northern Gulf of Mexico coast that does not have a channel of some kind.

Generally, the larger channels are perpendicular to the coastline and traverse an estuary from its connection with the sea to its headwaters. Barge channels usually parallel the coastline, pass laterally through an estuary and continue across marshes and uplands to connect with another estuary. The smaller channels usually afford transport from the shallow shoreline zone or small tributary to deeper waters of an open bay or to a larger channel. Thus, as estuary frequently is criss-crossed by many channels of different dimensions. The present trend is to enlarge existing channels and to construct more new large channels to accommodate the bigger vessels and barges that are being put into service.

As the channels in an estuary develop, they eventually occupy every conceivable type of habitat or zone—the tidal connection with the sea, open bays, oyster reefs, shallow shoreline zones, beaches, tidal flats, beds of submerged aquatic vegetation, adjacent brackish marshes, river deltas, and tributary streams. All of these zones are part of the estuarine ecosystem and it is almost impossible to modify or rearrange one zone without modifying the others.

How do channels and the resulting spoil affect the estuarine ecosystem? Are these effects always bad or can they be good? Can a channel be modified to reduce or eliminate adverse effects? Can a channel be planned so that the environment is improved for fish and wildlife? Is there a right way and a wrong way to construct a channel and dispose of the spoil? The estuarine manager and conservationist deals with all these questions daily. Sometimes, answers are readily available. Too frequently, however, solutions are not apparent and a search of the literature confirms the inadequacy of our state of knowledge about channels and spoil in relation to the estuarine environment and the fish and wildlife resources harbored therein.

PURPOSE OF CHANNELS AND SPOIL

When we think of channels, most of us immediately think of navagation. When we think of spoiling, we envision a large hydraulic dredge discharging sediments on spoil mounds in a bay. Certainly when a channel is dredged, the resulting material must be disposed of in some manner.

Channels, however, are dug for many purposes other than navigation. Frequently, a channel (called a borrow pit) is created incidentally to obtain fill material to form new land in a bay or to raise the level of adjacent marshes. Channels also are dug to drain wetlands, accommodate pipelines, provide for waste disposal, transport water, create waterfront property, obtain minerals or buried shell, improve sport fishing, and for many other reasons. Regardless of why a channel is dug, however, two basic alterations to the estuarine environment are evident for all: (1) channels deepen a portion of the estuary and (2) spoil tends to reduce water depths (Kutkuhn, 1966). It is evident, therefore, that many of the problems and benefits associated with navigation channels apply equally to channels dug for other reasons.

METHODS OF CHANNEL CONSTRUCTION AND SPOIL DEPOSITION

The two basic methods of channel dredging are mechanical and hydraulic; modifications permit varying degrees of control over resulting spoil materials (Table 1).

Mechanical dredging by bucket dredge or dragline is used for construction and maintenance of small channels. Spoil can be relatively well controlled in a small area. This control is frequently desirable from a fish and wildlife standpoint, particularly when spoil is to be placed in shallow bays and brackish marshes instead of on adjacent uplands.

Hydraulic dredging is usually employed for construction of the larger channels, through deeper open-water areas, and for large maintenance operations. Spoil areas are necessarily large and proper control of spoil requires use of enclosed ponding areas. Ponding areas, however, usually are not practical in open, deeper water; thus, spoil is dispersed widely over the affected water bottoms.

As indicated in Table 1, the several methods of dredging that are available offer considerable latitude for disposition and control of resulting spoil.

PROBLEMS WITH CHANNELIZATION AND SPOIL DEPOSITION

The biological value of estuaries and their role in perpetuating fishery resources are well documented (Chapman, 1966; Clark, 1966; Diener, 1965; Gunter, 1967; McHugh, 1966, 1967; Skud and Wilson, 1960; Stroud, 1967, Sykes, 1965; and Sykes and Finucane, 1966). The literature dealing with the effects of channelization and spoil dumping in estuaries, though extensive, frequently lacks documentary evidence.

The influence and effect of channelization and spoil on the physical and chemical characteristics of an estuary can be measured precisely, but interpretation of the effects of the changes on the biota are extremely difficult. Few detailed studies have been undertaken to determine precisely how, when, where, and why the biological environment of an estuary is modified by physical and chemical change. Surprisingly, specific examples of direct loss of estuarine water areas and brackish marshes by deepening and filling, although not hard to obtain, have not been evaluated precisely. Probably the most disrupting and critical influence of channels and spoil in the estuarine environment is the direct physical loss of habitat. Measurement of habitat loss, therefore, gives some quantitative evidence of the rapid destruction of our estuaries.

TABLE 1—DREDGING EQUIPMENT AND SPOIL DEPOSITION

Dredging equipment and method	Principal use	Disposition of spoil	Spoil control	Comments
Mechanical dredge Bucket and dragline	Small channels	Place adjacent to channel	Small spoil area; minimum turbidity	Usually the preferred method; problem exists of blocking drainage and reducing water exchange or circulation
		or		
		Place on barge	Remove from site	High cost usually prohibitive
Hydraulic dredge Hopper	Large channels	Remove from site to designated spoil area of preferably low-value habitat	Excellent at site; moderate at discharge point where turbidity is frequently high	Used where spoil area is not available near site or where adjacent spoil deposition would increase maintenance dredging
Pipe discharge	Large and medium size channels	Place in mounds adjacent to channel	Very poor unless spoil is retained by ring levee. Turbidity is high without ring levee and spoil area is large	Danger exists of segmenting bays and blocking drainage, tidal exchange, or circulation. Destruction of shallow bay and marshes by filling creates a major problem
Side broadcast discharge	Large channels	Scattered in layer over large area of bottom adjacent to channel	Depth of spoil on bottom can be controlled. Spoil area is large, turbidity is high, and silt is dispersed by currents	Can prevent bay segmentation but very large areas of water bottoms can be silted. Needs more study

Recently, gross measurements (U.S. Fish and Wildlife Service, 1967) reveal that dredging and filling have destroyed more than 200,000 acres of shallow bay nursery areas in Gulf and south Atlantic estuaries over the past 20 years. This figure does not include areas of coastal marsh which have been destroyed.

Schmidt (1966) reported that 45,000 acres of tidal marshes were destroyed between Maine and Delaware from 1954 to 1965. Spoil from dredging navigation channels and boat harbors accounted for 34 percent of this loss. Rounsefell (1964) reported that a single project in Louisiana, the Mississippi River-Gulf Outlet Channel, destroyed 23,606 acres of marsh and shallow-water nursery areas (17,058 acres by spoil deposition and 6,548 acres by deepening). Loss of habitat in the larger open bays and sounds near the Gulf of Mexico was not included in Rounsefell's figures. About 20 percent of the total surface area of Boca Ciega Bay, Florida, has been buried under waterfront lots (unpublished data, Bureau of Commerical Fisheries Biological Laboratory, St. Petersburg Beach, Florida) and in San Francisco Bay, 192,000 acres of formerly important estuarine habitat have been reduced to 37,000 acres, mostly by filling (Delisle, 1966).

On the basis of recent reports and maps (U.S. Army, Corps of Engineers, 1966a and 1966b), about 700 miles of Federal navigation channels in Texas have modified more than 13,000 acres of shallow bay estuarine nursery areas and destroyed almost 7,000 acres of marsh by deepening. Spoil from excavation of these channels destroyed an additional 23,000 acres of marsh and more than 55,000 acres of shallow bay areas (Table 2). The destruction of vital bay and marsh nursery areas in Texas from dredging of private channels for navigation and from other projects is not known, but must be great.

TABLE 2—ESTIMATED AREA OF ESTUARINE ZONE IN TEXAS DESTROYED OR SEVERELY DAMAGED BY EXCAVATION AND SPOIL FROM FEDERAL NAVIGATION CHANNELS

Type of habitat	Channel Length (Miles)	Channel Area (Acres)	Spoil Area (Acres)	Total Area (Acres)
Open bay waters	282	7,590	30,320	37,910
Bay shoreline zone	178	5,690	21,310	27,000
Tidal flats	36	920*	3,920	3,920
Marshes	193	6,980	23,000	29,980
TOTAL	689	20,260	78,550	98,810

*Not included in totals.

The Galveston Bay estuarine system is the largest and most important in Texas; it contains some 430,000 acres of surface water and brackish marsh. To date, about 67,000 acres of this valuable estuary have been physically destroyed, severely damaged and rearranged, or isolated. Channels and resulting spoil have accounted for 56 percent of this damage (U.S. Fish and Wildlife Service, in press).

Unfortunately, the examples of estuarine destruction which I have cited are being duplicated in most of the estuaries along the Gulf and south Atlantic coasts. Such losses of vital habitat are appalling, since it is nearly impossible to replace or restore these areas once they have been destroyed (Ford, 1960; Delisle, 1966). This problem was aptly summarized by Clark (1966) who stated, "This abundance of life [referring to the fishery resources of Atlantic coastal waters] is dependent upon the fertilizing effect of the coastal wetlands and protection they offer to many forms of life. The loss of any shallow coastal area will in some measure diminish life in the sea."

In addition to the direct physical loss of habitat, channelization and spoil deposition can modify the physical, chemical, and biological characteristics of the estuary in many other ways. The changes may be either beneficial or destructive, depending upon the particular estuary, the resources in question, or the point of view of the person reporting the change.

One of the first recorded complaints concerning canal dredging on the Gulf coast was recorded by Cary (1906). He reported that the many canals being dredged in the Louisiana coastal marshes were allowing large amounts of fresh water to enter the coastal bays during freshets, causing salinity reduction to levels dangerous for oysters. We seldom hear such complaints any longer. Instead, the waters in many areas are becoming too saline for oysters (McConnell, 1952a and 1952b; St. Amant, et al., 1956). The problems of increased salinity in Louisiana from channel construction were discussed by St. Amant, Friedrichs and Hadju (1958) as follows: "In recent times an increasing number of canals and deep water channels with their spoil levees have been cut across the marsh both laterally and vertically. This has resulted in changed direction of water flow, the damming of flow by levees, and has greatly increased the velocity of salt water flow into the marsh and fresh water flow through the marshes to the sea. The net result has been drastic increases in salinity in some areas and a rapid deterioration of productive marsh and bay conditions."

Numerous other examples of increased saltwater instrusion via deep channels have been studied or reported. Deep channels permit high-salinity waters from the sea to penetrate the upper reaches of an estuary and disperse throughout its area. Such a situation frequently develops in the Galveston estuary, Texas, during low river flow (Fig. 9).

One of the more striking examples of saltwater intrusion is that caused by the Mississipi River-Gulf Outlet Channel in Louisiana. This channel has helped high-salinity waters from the Gulf of Mexico to penetrate and disperse throughout thousands of acres of marsh and shallow bays and even has caused salinities in the 640-square mile Lake Pontchartrain to increase manyfold. The problem of saltwater intrusion via the Mississippi River-Gulf Outlet Channel was first predicted from a hydraulic model study (U.S. Fish and Wildlife Service, 1962; Tallant and Simmons, 1963), was discussed by Rounsefell (1964), and confirmed by subsequent field sampling

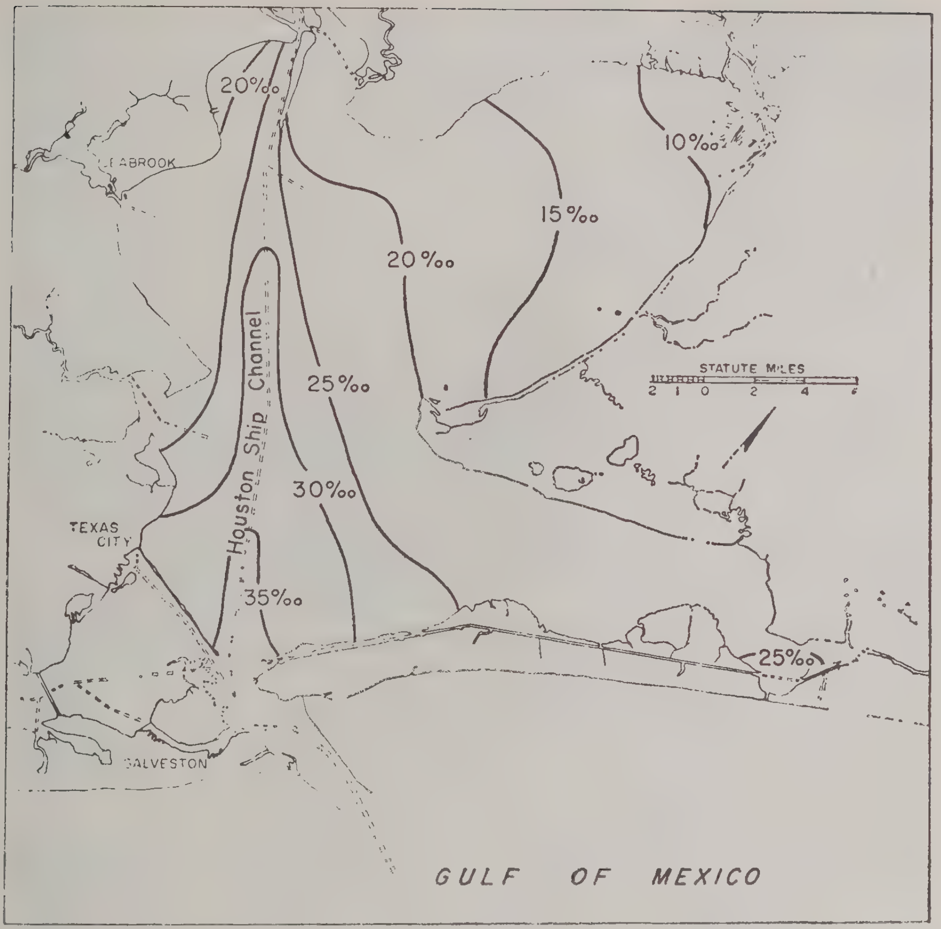

Figure 9—Salinity intrusion (at the bottom, in parts per thousand) into Galveston Bay, Texas, via the Houston Ship Channel in January 1963 during low river flow.

(Corps of Engineers and U.S. Fish and Wildlife Service, personal communication).

Considerable knowledge has been accumulated on salinity characteristics of estuaries and the factors that control them (U.S. Army, Corps of Engineers, 1965). It is now possible to predict changes in major features in the salinity regime of certain types of estuaries that would accompany channel construction or channel modification (French, 1960; Ippen and Harleman, 1961; Sakou, 1963; Simmons and Lindner, 1965). Unfortunately, conservationists are not as yet using this knowledge to best advantage.

The modification by channels of tidal exchange between an estuary and the sea can have far greater consequences than merely encouraging or reducing salt-water instrusion. Tidal currents, assisted by wind, furnish the energy for horizontal translation and mixing throughout an estuary. Increased tidal velocity tends to convert a stratified estuary to vertical homogeneity (Pritchard, 1955). Problems of excessive algal blooms in Great South Bay and Moriches Bay, New York, which seriously reduced oyster producing capacity, were studied by Ryther (1954) and Ryther et al. (1958). Considerable improvement resulted when Moriches inlet was reopened to restore effective exchange with the sea. Odum and Wilson (1962) noted the possibility that bays with little flushing may develop higher productivity and more effective regeneration of nutrients. Perhaps this is one of the reasons why Gulf estuaries in which the tides are small are so productive.

Segmentation of bays by channels and spoil banks can also cause serious derangements. Large areas of shallow water and brackish marsh frequently are isolated to be as effectively lost for nursery areas as if they were physically destroyed. Kutkuhn (1966) noted that deposition of spoil from channel dredging may subdivide a bay in such a way that subsequent changes will render the segmented portions shallower and less useful as nursery areas. Shoaling has become so serious in Lake Grand Ecaille and Bay Long, Louisiana, because of severe silting caused by bay segmentation, that boats can no longer operate out of marked channels (Waldo, 1958).

Problems arising from increased turbidity and sedimentation differ among estuaries. Obvious damage from high turbidity may occur in one estuary but not even be noticed in another. It is necessary, therefore, to characterize an estuary before describing the effects of turbidity and sedimentation. Most Gulf and south Atlantic estuaries can be placed in two broad categories, each of which is affected differently by increases in turbidity and sedimentation. These categories may be described as follows:

1. Receives considerable tributary fresh water containing large amounts of sediment. Waters, therefore, are relatively turbid naturally and a well-defined salinity gradient (from nearly fresh water to sea water) is usually present. Beds of submerged aquatic vegetation are scarce, if present at all, but emergent vegetation forms large areas of bordering brackish marsh. This type of estuary, which is very productive, is almost continuous from Galveston Bay, Texas, to Mobile Bay, Alabama.
2. Salinities are relatively high and waters comparatively clear. Tributary discharge and accompanying sediment loads are small in relation to size of the estuarine basin. Very little bordering marsh is evident, but extensive beds of submerged aquatic vegetation are present.

In the naturally turbid estuary, increases in turbidity, which frequently are temporary and local, are difficult to detect and often are not noticed. Once silt is put into suspension by dredging it behaves as if natural suspending agencies (wind, waves, flooding, tide) put it there (Mackin, 1961). Because the heavier material put into suspension settles quickly, turbidities a short distance from the spoil site rarely exceed natural levels caused by wind (Cronin, 1967). Mackin (1961) reported that turbidities 300 feet from the discharge pipe of a hydraulic dredge did not exceed those observed on occasion under natural conditions in a naturally turbid Louisiana Bay. He also stated that the amount of fines (silt and clays) drifting away from the spoil site did not exceed 1 percent of the total materials removed. With increasing distance from the spoil area dilution was very effective in reducing turbidity.

The problems of increased turbidity in the clear-water estuaries that have large beds of submerged aquatic vegetation, however, are entirely different. Even temporary increases in turbidity can cause serious damage. Turbidity obviously interferes with light transmission and photosynthesis and usually increases oxygen demand (Odum and Wilson, 1962). The reduced penetration of sunlight will cause beds of submerged aquatic vegetation to die and prevent them from becoming reestablished. Periods of high turbidity are frequently prolonged because wave action erodes spoil banks and resuspends fine sediments which have settled on nearby bottoms. Even after spoil areas have stabilized, periodic maintenance dredging can perpetuate the problem indefinitely.

The rearrangement of bottom sediments by siltation can also have a disturbing influence on an estuary. The heavier particles put into suspension by a hydraulic dredge settle out within a short distance but the remaining fine material can be carried considerable distances and "coat" a large area of bottom—even form a "false" bottom that will not support benthic animals (Hollis et al., 1964). Usually, however, fine materials become part of the total sediment structure of an estuary to be continually rearranged, shifted, and transported seaward by waves and currents. In a shallow Louisiana bay, Mackin (1961) reported that silt was carried and deposited as far as 1,300 feet from a working dredge. Wilson (1950) reported that silt extended about 300 yards from a hydraulic shell dredge working in a Texas bay. Hellier and Kornicker (1962) discovered that sediments discharged from a hydraulic dredge during construction of the Gulf Intracoastal Waterway were carried at least one-half mile where they were deposited to a depth of 22 centimeters in 1 week and 33 centimeters within 18 months.

Much of the information presently available to the biologist concerning channelization and spoil was obtained from study of the effect of increased turbidity and silting on oysters and from attempts to prove that the oyster is a hearty creature capable of surviving extreme abuse. Almost ignored in these studies was the direct physical destruction of shallow bays by deepening and filling. What good results from proof that a temporary increase in turbidity did not harm an oyster when the spoil deposit which promoted the turbidity destroyed hundreds of acres of bay or marsh? It is about time things were put in their proper perspective.

BENEFITS FROM CHANNELIZATION AND SPOIL

Channel construction in a shallow bay or brackish marsh frequently can benefit the fishery resources even though some habitat may be destroyed by spoil. Channels can and do connect isolated waters and marsh areas with the estuary proper to enlarge the estuarine nursery area. Channels have opened up considerable nursery areas in Louisiana and Texas. Much of the coastal marsh between Sabine Lake and Galveston Bay, Texas, was formerly isolated and not available to estuarine animals. Dredging of the Gulf Intracoastal Waterway across 40 miles of this marsh opened thousands of acres of nursery area to estuarine shrimp, crabs, and fish. Unfortunately, some of this marsh since has been reisolated to prevent salt-water intrusion into nearby rice-growing areas.

Because many estuarine areas are partially isolated or far removed from a source of saltwater, they have extremely low salinities and provide nursery habitat for very few species. The penetration of these areas by channels frequently is accompanied by increases in salinity that permit more species to be accommodated. The danger exists, however, that salinity will be increased so much as to alter the habitat adversely, particularly the vegetation. Improvement of habitat conditions by saltwater intrusion to a specific area often is accompanied by habitat deterioration elsewhere from excessively high salinity.

Severe winter storms locally called "northers," have caused massive fish kills in the shallow Texas bays (Gunter, 1941; Gunter and Hildebrand, 1951). The deeper waters in channels do not chill as fast as shallow bay waters and thus provide fish with a route of escape or refuge. The 30-foot-deep Offatts Bayou in Galveston Bay is noted for its excellent sport fishing during and following winter storms.

The Gulf Intracoastal Waterway through the Laguna Madre of Texas now provides an avenue of escape for fish from both cold and the excessive hypersaline conditions that develop in summer from high evaporation (Simmons, 1957). The Gulf Intracoastal Waterway has also improved water circulation in the Laguna Madre and thus has lessened excessive hypersalinity (Breuer, 1962). Salinity greater than 100 parts per thousand was reported by Collier and Hedgpeth (1950) before construction of the Gulf Intracoastal Waterway, but since has not exceeded 80 parts per thousand (Simmons, 1957; Breuer, 1962).

Another benefit attributed to channel construction is the release of nutrients bound in the bottom sediments (Gunter, 1967). Although Gunter (1957) recognized that the deleterious effects from spoil are real, but localized, he hypothesized that the release of nutrients may more than offset the damage done.

PLANNING FOR CHANNELS AND SPOIL DEPOSITION

The Bureau of Commercial Fisheries in cooperation with the Bureau of Sport Fisheries and Wildlife and State conservation agencies reviews the plans for all channel construction in the nation's estuaries. When it is evident that channel construction and spoil deposition or both will have deleterious effects on fish and wildlife resources or the estuarine environment, a report is prepared and submitted to the Corps of Engineers. Each report contains an appraisal of the problems the project would generate and specifically states how and to what extent fish and wildlife resources would be adversely affected. The report concludes with specific recommendations for modifying project plans to reduce or eliminate anticipated project damage. Occasionally, it is possible to include recommendations to improve fish and wildlife habitat.

The reports for Federal navigation channels are directed to, and coordinated with, the District Engineer responsible for a particular project. For private projects requiring a Federal permit for construction in navigable waters, the Corps of Engineers forwards the recommendations of the Fish and Wildlife Service to the applicant. If the applicant agrees to the recommendations, he modifies his proposed plan, resubmits his application to the Corps of Engineers, and is then issued a permit. Frequently it is necessary for the applicant and the Fish and Wildlife Service to discuss the recommended modifications and agree to a compromise. If a compromise cannot be reached or if the applicant refuses to consider the recommendations, the decision to issue the permit rests solely with the Corps of Engineers.

In the review of plans for channel construction and spoil deposition, several factors must be considered and questions asked. Is the channel alignment satisfactory or should it be moved? Will saltwater intrusion be a problem? Will excessive drainage result? Will turbidity increase enough to be damaging? How much high-value habitat will be destroyed? Is there a better way to handle the spoil? Will oyster reefs be damaged? How many waterways will be blocked and how much habitat isolated? Will segmentation of a bay be a problem? Will nearby isolated habitat be connected to the estuary? Will water circulation or tidal exchange be modified adversely? Will natural waterways and tributaries be destroyed or usurped? These are but some of the questions that must be asked when appraising each proposal for channel construction and deposition of spoil in the estuaries and marshes. Finding answers to such questions or solutions to the problems they pose can be extremely difficult; a simple solution usually is not available.

On the basis of review of hundreds of channel projects, however, we have developed general guidelines and criteria to assist us to formulate recommendations for project modification to serve the fish and wildlife resources. These guidelines and criteria are not intended to be all inclusive, nor are they minimum or maximum standards that must be adhered to absolutely. Furthermore, they best can be applied by the trained biologist who is familiar with the area in question.

1. Channels should not cross nor should spoil be placed on high-value habitat. High-value habitat in most estuaries includes, but is not limited to, brackish marshes, vegetated shoreline zones, beds of submerged aquatic vegetation, protected shallow waters near shore, oyster reefs, and small meandering tributaries (bayous) in the tidal zone.
2. To provide for maximum water exchange and circulation, spoil should be placed in mounds at least 1,000 feet apart on alternating sides of a channel.

3. Spoil should not be placed in the water closer than 500 feet from the shoreline of shallow, protected bays.
4. Natural drainage channels and waterways should not be blocked by spoil. Isolation of an area is far more damaging than changes in the environment which may result from salt-water intrusion.
5. The integrity of natural waterways should be maintained. This principle is especially applicable to dead-end access channels and pipeline canals.
6. Spoil should be placed on uplands (above mean high tide) where possible; otherwise it should be confined by ring levees, if necessary, to as small an area as practical.
7. Spoil deposition sites should be retained for future maintenance spoil.
8. Where possible, isolated waters and marshes should be connected to the estuary to enlarge the area of nursery habitat.

HABITAT REHABILITATION

Every opportunity should be taken to study and develop methods for rehabilitating estuarine areas which have been severely damaged or destroyed. The indiscriminate dumping of millions of cubic yards of spoil from channel excavation has destroyed submerged aquatic vegetation, marshes, and shallow bays. The shorelines of spoil "islands" usually are unstable and devoid of emergent plants. Shallow flats created by spoil deposition seldom develop a vegetative cover. If beds of submerged aquatic plants can be reestablished or if emergent vegetation can be made to grow along the hundreds of miles of barren shoreline, surely the productiveness of our estuaries will remain high or be improved.

To accomplish this rehabilitation, however, we must learn how to control excessive turbidity and to stabilize shorelines. We must learn how to reestablish submergent vegetation economically and how best to vegetate barren shorelines. Perhaps the method of spoil disposal can be controlled to facilitate the growth of vegetation.

The entire field of habitat rehabilitation promises to yield great rewards but unfortunately has been sadly neglected. We know that thousands of acres of estuarine habitat have been damaged and destroyed and that the future promises an increase of this problem. It is time now to stop, and if possible, to reverse this destructive trend. Habitat rehabilitation certainly is one way to accomplish this goal.

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Estimation of Fur Seal Pup Populations by Randomized Sampling

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ABSTRACT

It is well known that usual tag-sample estimates are valid if it can be assumed that the sampling process is random with respect to the presence or absence of the tag. This may occur because of natural processes or it may be the result of deliberate design of the experiment either in the tagging phase or in sampling, or in both. Procedures of this type, which have been applied to estimate the population of young Pribilof fur seals, are discussed. Particular consideration is given to variance estimates, comparisons of sample size, and methods of determining the randomness of allocation of the tags.

INTRODUCTION

The aim of this paper is to review a method of population estimation through tag-sample or capture-recapture procedures in which the assumptions required for validity of the usual estimates cannot be assumed to hold. If the tagging or sampling procedure is properly randomized, valid estimates are obtainable, though the formulas may be different from those usually employed in tag-sample procedures, particularly in respect to variance estimates. Because this method was developed to estimate the population of Pribilof fur seals, it is discussed primarily in reference to this species. We believe that the procedures and ideas may be widely applicable in wildlife and fish populations where failure of subgroups to mix properly causes doubt of the validity of the usual estimation procedure based on a Petersen or Lincoln index. The ideas of randomized sampling procedures and the formulas of cluster sampling are not new but have been widely used in many sampling problems, even perhaps in population work. We do not think that these ideas have been given sufficient explicit recognition and wish to call further attention to them and to their development and use in fur seal research.

A primary purpose of population dynamics research on fur seals is to determine what number of young seals (pups) will produce the maximum sustainable yield of salable skins at age 2 and older. To do this, it is necessary to estimate accurately the number of pups born. Numerous methods have been used to estimate the pup population. Direct counts of pups were made in the early 1900's, when the population was low. As the population increased, accurate total counts became impractical on some rookeries and other methods had to be found.

The last complete count was in 1922, though a partial count was made in 1924. Thereafter, until 1947, the pup population was estimated by extrapolation from the earlier complete counts. By the late 1930's this extrapolation was no longer valid and alternative methods of estimating the number of pups were sought. A tagging experiment, begun in 1941, was interrupted by World War II. Tagging on a large scale was resumed in 1947; tags placed on male pups were recovered in the male kill at ages 2 through 5 (mostly at ages 3 and 4).

Other methods were tried, at the same time, to provide estimates for comparison with the tagging estimates. For example, direct sample counts were obtained on the ground and from aerial photographs and were extrapolated in various ways. Early estimates from tagging were reasonable and consistent with one another and with these direct estimates (Kenyon, Scheffer, and Chapman, 1954).

By the mid-1950's, tagging estimates became excessively high and fluctuated erratically (Chapman, 1958; 1964). Research was undertaken to determine the reasons for these unsatisfactory estimates and over the past several years many improvements have been made in the tagging and recovery methods. One problem that could have caused inflated estimates is that tagged pups have poorer survival than untagged ones. Furthermore, since the method depends on recoveries made in the commercial kill, a 3-year lag thus falls between the time of tagging and the first reliable estimation of the pup population.

For these reasons, a different method of estimating the pup population was needed. The first attempts to develop the marking and sampling method described here were made in 1960. This method has now been developed sufficiently to provide satisfactory estimates with adequate precision and tolerable variability.

DEVELOPMENT OF THE METHOD

A brief description of the behavior of adult male seals and pups is necessary to understand fully the problems involved in the development of this method. Adult males are polygamous and hold breeding territories on the rockeries. The pups, which are born mostly in late June and early July, begin by early August to congregate in large, nearly homogeneous groups (pods). They do not move extensively and the different pods mix only slightly. They continue to nurse throughout August, September, and October. In early November they leave the islands and attempt to make the transition to the marine environment of the Bering Sea.

The estimation of an animal population through mark-sample (capture-recapture) methods requires that the sampling process be random with respect to the mark, i.e., that the chance of an animal being recaptured is independent of whether it bears a mark. Such randomness is assumed to occur in nature, if there is thorough mixing of all the animals between marking and sampling. In the case of the tag-sample experiment conducted on fur seals from 1947 through the 1950's, it was assumed that the mixing would take place in the interval of several years elapsing between marking and recapture.

On the other hand, this time lag of approximately 3 years could be eliminated if fur seal pups could be tagged and sampled during their first few months of life, while they are still on land. In view of the lack of natural mixing during this period, in order to provide valid estimates, the mark-sample process had to be designed so that randomness would be inherent in the process. Such randomness can be achieved by proper distribution of the tags or by appropriate allocation of the samples, or by both.

In most tagging experiments with young fur seals through 1960, the tags were applied to pups in a few conveniently located pods on each rockery and with little mixing of the pods, the distribution of tags was extremely clumped. Attention was therefore given first to choosing sampling stations randomly and hence independently of the presence or absence of tagged animals.

Experimentation with such random sampling was initiated when a number of sampling stations were randomly selected and marked on two rookeries of St. Paul Island in 1960. The sampling procedure was to count the number of tagged animals in a group of 25 nearest each sampling station. It was presumed that any single cluster of 25 would be far from random; in fact, it was expected to show almost all marked or almost none marked. On the other hand, it was hoped that if the sampling stations were properly distributed throughout the rookeries, the average of all samples would be a reasonable basis for estimating the total population. In other words, the sampling scheme was designed to compensate for the lack of mixing of tagged and untagged pups.

The 1960 experiment was sufficiently promising to warrant extending the procedure to all of the St. Paul Island rookeries in 1961. Expansion of the program in 1961 also included trial and evaluation of two methods of sampling and two sizes of samples. One method was to gather into a single pod more than 100 pups which were then permitted to escape between two observers who counted them to obtain the ratio of tagged to untagged animals. In the other method of sampling, an observer counted groups of 25 pups at equal intervals along parallel transects perpendicular to the water. No difference was detected in the variance between samples of 25 and 100 pups in this expanded program. Since counting of 25 pups is easier and quicker and permits a large number of samples, this procedure has been used in subsequent years.

Experience gained during sampling in 1961 and again in 1962, however, suggested that a method of marking other than tagging was needed because the tags could not be detected easily. Though some early marking of fur seals was done by shearing or hot-iron branding, all of the marking studies used for population estimation from 1941 through the early 1960's utilized a cattle-ear tag and an identifying checkmark on one of the flippers. Although the checkmark and the tag are easily observed on the carcasses of commercially harvested animals, they are not so easily detected on unrestrained live animals.

Beginning in 1963, pups were marked by shearing the black guard hair from the top of the head to expose the light underfur. This method not only produced an easily identifiable mark that could be seen without difficulty by the samplers; but with this simpler marking operation, it was no longer necessary to round up pods of animals and drive them to a holding pen to mark them, as had been the case when applying the cattle-ear tag and checkmark. This made it possible to distribute marks throughout the rookeries and hence opened up the possibility of random allocation of marks as well as random allocation of samples.

In 1962 and later years, all rookeries on St. Paul Island have been sampled at least twice; the duplicate estimates achieved provide an additional approach to the estimation of the variance of the population estimate. The pups on two areas were also counted in 1963 to check the accuracy of the estimates based on marking and sampling. The 1963 data showed that the distribution of marked animals in the sample deviated considerably from a binomial distribution, suggesting that random allocation of marks had not been attained and that additional effort was needed to distribute the marks more evenly throughout the rookery.

In 1964 and 1965, the techniques generally were the same as used in 1963, except that more effort was exerted to obtain a better distribution of the marks. In 1965, each rookery was subdivided into smaller units and the number of harem males were recorded for each unit. The number of marks to be applied in each unit was allocated on the basis of the counts of harem males. Also, the number of areas in which the total number of pups were counted to check the accuracy of estimates was increased to four. The four areas contained 12% of the estimated total number of pups.

In 1965 all rookeries were sampled three times. In the third sampling, pups were counted in groups of 100, as in 1961, to test whether or not, with the more even distribution of marks, an increase in sample size would improve the estimates and decrease variance. This did not prove to be the case, confirming the 1961 results.

METHODS OF ANALYZING RECAPTURE DATA FROM RANDOM PLACEMENT OF MARKS OR RECAPTURE EFFORT

In the early years of these experiments, primary emphasis was placed on allocation of systematic samples throughout the area inhabited by the young fur seals, so that a meaningful estimate could be obtained despite the fact that the tags had been placed in clusters. Such an estimate would not be derived from either the usual or modified

Petersen ratio $\left(\frac{(M+1)(n+1)}{m+1}\right)$

where M = number of marked animals
n = number of animals sampled
m = number of marked animals recaptured in the sample.

With such cluster samples, the proportion marked would be estimated by

$$\bar{p} = \frac{1}{k}\sum_{i=1}^{k}\frac{m_i}{n_i} \qquad (1)$$

(cf. Cochran [1963], p. 247)

where

m_i = number of marked animals in the i^th^ sample
n_i = number of animals in the i^th^ sample
k = number of samples.

Finally $\hat{N} = \frac{M}{\bar{p}}$, where $\hat{N}$ is the estimate of the population size N. . . . (2)

If the sample size is constant, however, $n_1 = n_2 = \ldots = n_k$, then this does become the usual Petersen estimator.

If the samples are small and few, some bias correction would clearly be desirable (comparable to the modification in the Petersen ratio of $\frac{Mn}{m}$ to $\frac{(M = 1)(n + 1)}{m + 1}$). In this study, the number of samples amounted to several hundred and the number of mark recaptures in all samples to some thousands, so that no bias correction was considered necessary.

There are two ways of calculating the variance of cluster estimates. First, the usual approximation of the so-called delta method yields:

$$\text{var } \hat{N} = \frac{M^2}{\bar{p}^4} (\text{var } \bar{p}) \qquad (3)$$

where

$$\text{the var } \bar{p} = \frac{\sum_{i=1}^{k} (p_i - \bar{p})^2}{k(k-1)} \qquad (4)$$

if the finite population correction is ignored.

A second method of estimating the variance is through interpenetrating samples. In this procedure, the total sample is subdivided randomly into a number of subsamples from each of which an estimate is obtained. Denote by

$\hat{N}_i$ = the estimate of the population from the i^{th} subsample or replicate

and by

$$\hat{N} = \frac{1}{r} \sum_{i=1}^{r} \hat{N}_i, \qquad (5)$$

$\hat{N}$ is the mean of the r replicated subsamples.

The estimated variance of $\hat{\hat{N}}$ is

$$\frac{\sum_{i=1}^{r} (\hat{N}_i - \hat{\hat{N}})^2}{r(r-1)} \qquad (6)$$

We note that $\hat{\hat{N}}$ calculated as the mean of the r subsample estimates may differ from $\hat{N}$ calculated from formula (2), i.e., from the total sample, though the difference is usually small.

The early sampling procedure was set up so that although the tags would be placed in clusters, i.e., nonrandomly, the sampling would achieve the randomness required. In these years most or all of a selected group of pups were tagged. With the replacement of the tag by the shearing mark, however, it was possible to attempt to place the marks randomly throughout the rookeries. This was accomplished by subdividing rookeries and allocating the number to be sheared on the basis of the numbers of adult harem males in each subarea. If complete randomness in the placement of marks was achieved, then the distribution of the samples would not be critical and the marks in the samples would be random, i.e., have a binomial distribution.

TABLE 1.—*Proportion of previously tagged seals in 83 successive samples of 100 pups, Gorbatch Rookery, 26 and 28 August 1961*

August 26	2, 0, 1, 6, 4, 33, 62, 49, 55, 38, 52, 77, 85, 54, 27, 17, 3, 3, 3, 2, 2, 1, 0, 0, 4
August 28	0, 0, 0, 4, 0, 0, 0, 12, 4, 8, 60, 48, 72, 72, 76, 80, 56, 44, 50, 56, 56, 28, 60, 36, 44, 44, 28, 52, 72, 28, 72, 60, 60, 84, 76, 52, 84, 48, 52, 60, 40, 12, 8, 12, 4, 8, 44, 16, 0, 8, 0, 0, 4, 12, 8, 0, 0, 0.

Analysis of the St. Paul Island Data.—Because the fur seal rookeries on the Pribilof Islands are distinct units, the total population estimate for St. Paul Island is the sum of the estimates for the separate rookeries and the variance of the total is the sum of the variances of the estimates for the several rookeries. Allocation of the number of pups to be marked on each rookery and within units of each rookery are based on counts of adult males having females.

A typical 1961 sampling is tabulated in Table 1 when tags were placed in clusters. The table lists 25 successive samples counted on 26 August and 58 counted on 28 August.

The interpenetrating or replicated subsamples were defined as follows:

Subsamples 1, 2, 3: Every third observation of 26 August beginning with observations 1, 2, 3, respectively.

Subsamples 4–10: Every seventh observation on 28 August beginning with observations 1, 2, 3, 4, 5, 6, 7, respectively.

Since there are 25 observations on 26 August, this yields subsamples of size 9, 8, and 8, respectively; the 58 observations on 28 August are subdivided into two subsamples

TABLE 2.—*Estimates of $\hat{N}_i$, $\hat{\hat{N}}$, and $\hat{N}$ for Gorbatch Rookery, 1961*

Subsample	Estimate $\hat{N}_i$
1	20,500
2	24,220
3	20,061
4	17,458
5	16,672
6	17,732
7	14,391
8	12,110
9	13,066
10	14,821
Total	171,031

$\hat{\hat{N}} = 17,\ 103$; estimated variance $(\hat{\hat{N}}) = 1,394,000$

$\hat{N} = 16,457$; estimated variance $\hat{N} = 2,932,000$ (from formula (2))

of size 9 and five of size 8. The resulting estimates of N_1 are shown in Table 2.

A summary of the estimates and of their variances for all rookeries on St. Paul (1961 data) are listed in Table 3.

It is to be expected that the replicate or subsample estimates of the population size based on small samples will be biased upward. This is reflected in that $\hat{\hat{N}}$ in Table 3 is somewhat higher than $\hat{N}$. On the other hand, the large difference between the variance from the cluster formula and the subsample procedure is unexpected. The cluster sample variance formula assumes that the samples were randomly selected but in fact they were chosen, in the present situation, on the basis of a systematic scheme. In these circumstances, the variance derived from the interpenetrating or random subsamples is perhaps the more appropriate one to use.

Since 1962 the samples have been completely replicated so that the variance can be estimated from the two estimates so obtained. This procedure assumes that the only difference in the replicates, taken usually about a week apart, stems from sampling errors. The estimates and the estimated variance of the estimates are shown in Table 4. The variance of the mean estimate will, as usual, be the variance of a single estimate divided by 2 (and in 1965 when three samples were taken, by 3).

The standard deviation of the estimate of the total St. Paul Island pup population, based on the pooled variance estimates of Table 4, is 22,068.

A review of the estimates in Table 4 suggests that the second estimate tends to be higher than the first. To test this possibility, a distribution free Hodges-Lehmann W test (1962) was applied, which is based on a comparison of ranks of differences of any estimate from the annual mean. For the 10 estimates, the differences of the early estimates rank 1, 2, 3, 4, and 6. The resulting W value has a probability of 0.024 under the null

TABLE 3.—*Estimates[1] of pup populations by rookeries on St. Paul Island, 1961*

	Number of animals tagged	$\hat{\hat{N}}$	Variance $\hat{\hat{N}}$ from formula (6) ($\times 10^{-3}$)	$\hat{N}$	Variance $\hat{N}$ from cluster formula (3) ($\times 10^{-3}$)
Zapadni	3,697	42,102	17,611	37,957	20,684
Reef	4,960	69,246	46,463	67,760	620,379
Lukanin-Kitovi	2,965	24,005	55,586	22,061	29,751
Little Zapadni	394	13,294	2,138	13,133	52,703
Gorbatch	4,965	17,103	1,394	16,457	2,932
Tolstoi	4,048	34,884	982	34,777	152,963
Vostochni	2,983	19,899	613	19,807	22,688
Polovina	4,280	21,663	579	21,583	32,208
Little Polovina	1,292	8,794	440	8,613	2,076
Morjovi	6,950	27,628	45	27,612	66,097
Zapadni Reef	2,925	5,850[2]	576[2]	5,850	576
Total		284,468	126,427	275,610	1,003,057

Standard deviation $\hat{N}$ (Total St. Paul Island) = 11,242

Standard deviation $\hat{N}$ (Total St. Paul Island) = 21,671

[1] Estimates based on samples of 100 pups.

[2] No estimate of $\hat{\hat{N}}$ and variance $\hat{\hat{N}}$ for Zapadni Reef because of small number of samples; estimates taken to be same as given by formula (2).

TABLE 4.—*Duplicate population estimates, St. Paul Island,[1] 1962–66 and their variances*

Year	Estimate 1	Estimate 2	Mean (1000's)	Estimated variance of mean (1000's)
1962	203,630	259,990	231.8	1,588,225
1963	227,301	232,926	230.1	1,582
1964	262,560	262,140	262.3	88
1965	208,468	220,821	225.7[2]	408,124
1966	262,736	292,300	277.5	437,015

[1] Excluding Sivutch Rookery (Sea Lion Rock).

[2] In 1965 a third estimate (247,960) is available based on samples of 100 pups. The mean shown is the mean of all three estimates.

TABLE 6.—*Results of chi-square computed for the binomial goodness-of-fit tests by year and sample, 1963–66*

	Sample 1			Sample 2		
Year	X^2	d.f.	Probability level	X^2	d.f.	Probability level
1963	297.1	48	<0.001	281.9	47	<0.001
1964	99.2	52	$<.001$	176.0	50	$<.001$
1965	138.7	56	$<.001$	36.0	50	.93
1966	57.9	41	.04	39.8	37	.35

hypothesis of no difference. Although a test suggested by the data must be viewed with considerable caution, it may be that one of the estimates has a slight degree of bias, e.g., this could be caused by differential mortality of marked animals, differential behavior of marked animals changing with time, or a number of other factors. Hence, the standard deviation (22,068), noted above, may be somewhat high.

Finally, Table 5 is a 1961 experiment comparison of estimated variances of $\bar{p}$ from large and small samples. Here, $\bar{p}$ is the mean proportion of tagged animals. Table 5 refers to a tagging experiment in which tags were applied in clusters and the component of variance from this clustering effect obscured any effect of sample size. It would be expected that as the marks were distributed more randomly throughout the rookeries, the component of variance associated with the clustering effect would decrease and the binomial component that is a function of sample size would become more noticeable. Studies have been made (McVay, 1947) to determine optimum sample size in such a cluster situation but in this experiment emphasis was placed on decreasing the clustering effect.

The results of tests on the goodness-of-fit of the observed distribution of tag recoveries to the binomial distribution that would be expected if the marks were randomly distributed are shown in Table 6. In 1965 and 1966, the distributions in the second sample exhibit a good fit to the binomial distribution, although the earlier samples did not.

Pup samples of size 25 and 100 were again obtained in 1965 when the distribution of the marks on the rookeries was approximately random. The variance for the samples of 25 seals was less than that for larger samples of 100 seals, on every rookery (Table 7). This difference was not what would be expected and it was not apparent why the large samples had the highest variance.

The estimates obtained from this sampling program, undertaken immediately after tagging, were initially much lower than the estimates derived from tag recoveries made in the commercial kill (3 to 4 years after the placement of tags). The estimates from tag recoveries in the commercial kill were in question, but it was not clear that the fall sampling estimates were unbiased. To check the latter estimates, complete counts were

TABLE 5.—*Comparison of estimated variances of $\bar{p}$ from large and small samples, St. Paul Island, 1961*

Rookery	Samples of 100	Samples of 25	
Gorbatch	0.0760	0.0823	
Little Polovina	.0176	.0259	.0230[1]
Zapadni	.0060	.0167	
Weighted average	.0379	.0382	

[1] October 21 sample.

TABLE 7.—*Comparison of the estimated variance of $\bar{p}$ from large and small samples, St. Paul Island, 1965*

	Samples of 25 (2d sample)			Samples of 100		
Rookery	Number of samples	Total number sampled	Variance ($\times 10^{-3}$) of $\bar{p}$	Number of samples	Total number sampled	Variance ($\times 10^{-3}$) of $\bar{p}$
Gorbatch	50	1,250	0.10	11	1,100	0.36
Reef	104	2,600	0.05	17	1,700	0.10
Polovina	13	325	0.44	6	600	0.63
Polovina Cliffs	56	1,400	0.10	12	1,200	0.67
Little Polovina	15	375	0.14	7	700	0.35
Vostochni	100	2,500	0.05	24	2,400	0.11
Morjovi	39	975	0.11	21	2,100	0.14
Tolstoi	106	2,650	0.05	16	1,600	0.20
Kitovi	34	850	0.17	8	800	0.24
Zapadni	105	2,625	0.04	13	1,300	0.23
Little Zapadni	75	1,875	0.05	9	900	0.29

TABLE 8.—*Comparison of counts and sample estimates on four rookeries of St. Paul Island, 1964–66*

Rookery	1964		1965		1966	
	Count	Mean sampling estimate	Count	Mean sampling estimate	Count	Mean sampling estimate
Kitovi (part)	1,095	1,382	1,248	1,225	–	–
Little Polovina	7,180	8,385	7,314	7,001	7,071	8,698
Morjovi (part)	17,530	16,880	18,384	15,874	17,388	17,948
Zapadni Reef	5,700	6,515	5,383	5,422	5,729	4,942
Total	31,505	33,162	32,329	29,522	30,188	31,588

made of the pups in sample areas. The counts and the fall sample estimates are compared in Table 8.

The differences between counts and estimates are within the range of sampling error of the estimates. Further, of the 11 estimates, 6 are in excess of the count and 5 below it, suggesting that the sampling procedure gives an unbiased estimate of what is actually counted. The counting is necessarily restricted to relatively smaller rookeries, for the most part, and may not represent conditions on large rookeries. Recent estimates from shearing and sampling, however, agree with up-to-date accumulative estimates based on the method discussed in Chapman (1964).

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1551

CHARACTERISTICS AND APPLICATION OF THE JERNE TEST IN STUDIES OF THE IMMUNE RESPONSE OF RAINBOW TROUT (SALMO GAIRDNERI).

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The successful application of the Jerne test to studies on antibody formation in rainbow trout was dependent on complement source and incubation temperature. Isologous complement and complement from closely related species was required. Temperatures between 4 to 20°C were most suitable. Fractionation of salmonid serum on Sephadex G-200 revealed that complement activity necessary for plaquing could be completely recovered in the second of three major peaks. The relationship of this fraction to the natural hemolytic activity of salmonid serum for mammalian red cells present in the first and third peaks is being investigated. Quantitation and qualitation of plaque formation was investigated using cells of various organs with particular emphasis on the spleen and anterior kidney. The plaques were of two types, large and small. Cells forming small plaques first appeared in the anterior kidney and later in the spleen. Cells forming large plaques showed the same sequence but appeared later than cells forming small plaques. Late in the immune response, the largest number of plaque forming cells was present in the spleen. (Supported in part by USPHS graduate training grant CA 5040 Natl. Cancer Inst.)

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The Cyclopterid Genus *Paraliparis*, a Senior Synonym of *Gymnolycodes* and *Eutelichthys*, with the Description of a New Species from the Gulf of Mexico

Daniel M. Cohen

The Cyclopterid Genus *Paraliparis*, a Senior Synonym of *Gymnolycodes* and *Eutelichthys*, with the Description of a New Species from the Gulf of Mexico

Daniel M. Cohen

Gymnolycodes **Vaillant and** ***Eutelichthys*** **Tortonese are shown to be junior synonyms of** ***Paraliparis*** **Collett. A diagnosis and a second record are presented for** ***P. leptochirus,*** **the type-species of** ***Eutelichthys. P. calidus*** **new species from the northern Gulf of Mexico is described and compared with its closest known relative,** ***P. bathybius*** **of polar seas.**

Introduction

PARALIPARIS is a genus of 25–30 described species of rarely encountered liparine fishes living mainly on the continental slopes and in the deep seas. This paper is a contribution to our knowledge of the taxonomy of the genus.

Paraliparis edwardsi (Vaillant)

The genus *Gymnolycodes* Vaillant was proposed for *G. edwardsi* from Morocco, and in the original description of both (Vaillant, 1888:312–315) was included in Lycodidae. However, in an appendix to the same volume, (p. 387), Vaillant removed the fish to the Discoboli and suggested that it might belong in *Careproctus* (now in Cyclopteridae or Liparidae). In his 1930 revision of Liparidae, Burke excluded *Gymnolycodes* (which he spelled *Gymnolicodes*) from the Discoboli on the basis of Vaillant's figure and description. Other authors have discussed *Gymnolycodes*, and their various opinions have been summarized by Tortonese (1959). To the best of my knowledge none of these authors has actually examined the only known specimen.

I have examined the holotype of *Gymnolycodes edwardsi,* and although it is badly damaged, certain critical characters were noted. It agrees with *Paraliparis bathybius* Collett (the type-species of *Paraliparis* Collett) in the following respects.

1. A tadpole-like shape.
2. Six, elongate, curved, sabre-like branchiostegal rays, the two most anterior far forward on the ceratohyal and separated from the posterior four.
3. The interopercle an elongate, curved bone resembling the branchiostegal rays.
4. The opercular bone greatly reduced, its most prominent remnant a flat spine or flap-like projection near the gill opening.
5. Gill opening small, completely above the level of the pectoral fin.
6. Sucking disc absent.
7. Pectoral fins divided into two sections.

8. Pelvic fins absent.
9. Dorsal, anal, and caudal fins confluent.
10. Vent far forward, between the pectoral fin bases.
11. Gill arches four, no slit behind the last.
12. Jaws with rows of close-set, conical teeth in definite series.
13. Post-cleithrum long and slender, easily visible through the skin.

In the original description of this species, Vaillant did not mention the lower segment of the pectoral fin. He postulated the presence of ventral fins, which he said had been torn away, and he described and illustrated the vent as being farther posterior than it actually is.

Gymnolycodes is clearly a junior synonym of *Paraliparis.*

Paraliparis leptochirus (Tortonese)

Because of Tortonese's (1959, 1960) comparisons of *Gymnolycodes* with *Eutelichthys* Tortonese, it seemed desirable to examine the holotype of *E. leptochirus* (the only known species), and Dr. Tortonese has graciously allowed me this privilege. I agree with him that *Eutelichthys* belongs in the Sclereoparei (Scorpaeniformes), for I confirm his observation of a prominent suborbital stay. He presented three differences that supposedly separate *Eutelichthys* from Cyclopteridae; they are listed and discussed below.

1. *The pectoral fins are not extended dorso-ventrally.* Close observation reveals a situation similar to that described by Johnsen (1919, figs. 7 and 4) in the cyclopterid species *Rhodichthys regina* (Collett) and *Paraliparis bathybius.* The pectoral fin in *Eutelichthys* is reduced from the broad-based, many-rayed structure found in most cyclopterids. However, the pectoral girdle is an elongate structure extending far anteroventrally to the main part of the fin. Near the anterior end of the girdle are two or three fragile rays lying beneath the translucent skin and not developed into a free fin. In addition, there is a rudimentary ray (as shown for *Rhodichthys,* fig. 7) between the two sections of the right pectoral fin. There is no doubt that *Eutelichthys* has a *Paraliparis* type of pectoral fin.

2. *The anus is immediately in front of the anal fin.* I find the anus well in advance of the anal fin—in fact between the pectoral fin bases as in *Paraliparis.*

3. *There is no ventral adhesive disc.* A disc is absent in the numerous species of the cyclopterid genus *Paraliparis* and also in the monotypic *Rhodichthys.*

The family name Eutelichthyidae is a junior synonym of Cyclopteridae and *Eutelichthys* is another junior synonym of *Paraliparis.*

Diagnosis of Paraliparis leptochirus.—Teeth simple, in bands. Middle pectoral rays rudimentary or absent; 12 rays in upper part of pectoral fin. Gill slit above level of pectoral fin base. Peritoneum dark; oral cavity light, but with some dark chromatophores. Dorsal fin with 3 predorsal pterygiophores + 46 rays; anal fin rays 45; vertebrae 9 + 46 = 48. Branchiostegal rays ~~5~~ 4 + 1 (possibly 2).

Additional material.—I have also examined three other specimens, trawled at 540–640 m near Banyul, France, approximately 400 miles north of the type-locality, off Alger. Although the French specimens are badly mutilated, they can be identified as *P. leptochirus.* The species is apparently a dwarf form, because one of the specimens, 51 mm SL, contained 35–40 eggs averaging two mm in diameter.

Paraliparis **calidus** n. sp.
Fig. 1.

Diagnosis.—Teeth simple, in bands. Middle pectoral rays rudimentary, widely separated; 15–18 rays in upper part of pectoral fin. Upper pectoral ray and opercular spine below a line through the horizontal diameter of the eye. Gill slit above level of pectoral fin base. Peritoneum dark; oral and branchial cavities dusky. Dorsal fin with 2 or 3 embedded +62–63 free rays; anal fin rays 57–58; vertebrae 10 + 57–60 = 67–70; caudal rays 6. Skin prickles absent. Rudimentary pores present on body.

Types.—Holotype: USNM 202469; 128 mm standard length; OREGON station 4662; 27°25′ N, 93°40′ W; 400 fms; 30 Jan. 1964; 40′ shrimp trawl. Paratypes: USNM 202471 (1♀), data as for holotype; USNM 202470 (1 ?, 115 mm SL; 1 ♀, 105 mm SL), OREGON 4149; 29°12′ N, 87°48′ W; 400 fms; 17 Dec. 1962; 40′ flat trawl.

Description.—Measurements are given in Table 1; counts in Table 2. A tadpole-like

TABLE 1. MEASUREMENTS OF *Paraliparis calidus* IN MM.

	Holotype	Paratypes		
	USNM 202469	USNM 202471♀	USNM 202470	USNM 202470♀
Standard length	128	–[1]	115	105
Depth at anal fin origin	21.3	19.6	15.4	16.2
Preanal	49.5	52.4	44.7	44.5
Lower jaw tip–vent	22.0	24.9	19.4	18.8
Vent to origin of anal fin	27.1	–	24.6	24.8
Head length to tip of opercle spine	25.2	28.7	23.6	22.9
Upper jaw tip to concealed end of maxillary	10.9	13.1	11.0	9.7
Horizontal diameter of unpigmented orbit	6.4	7.8	–	–
Upper pectoral lobe length	19.4	17.9	17.0	16.2
Lower pectoral lobe length	9.5	14.1	–	–

[1] Part of tail missing.

fish with the head and belly relatively wide and the body posterior to the anal fin origin compressed. Depth at anal fin origin 6.0–7.5 in standard length; head length 4.6–5.1 in SL; horizontal diameter of unpigmented orbit 3.7–3.9 in head. A single nostril located in front of upper half of eye. The jaws bear broad bands of small, even-sized teeth arranged in 7–9 regular oblique rows in the upper jaw and 10–12 rows in the lower; the teeth are wider than long and terminate in a single point. The maxillary extends to approximately the level of the midpoint of the eye; however, the posterior one-fourth of the bone is entirely sheathed. Branchiostegal rays elongate, curved, sabre-like; two on the ceratohyal, separated from the four posterior on the epihyal. Gill rakers absent; however, the lower arm of the first gill arch bears nine low bony tubercles. A prominent but weak two-ridged spine projecting posteriorly from the opercle above the base of the pectoral fin and in line with the lower third of the eye. Gill opening beneath the spine, entirely above the level of the pectoral fin.

The upper lobe of the pectoral fin on a broad, fan-like base, one to three very short or rudimentary rays between the upper and lower lobes; lower lobe of the pectoral fin consisting of three rays which are free distally, is far forward on the anterior extension of the pectoral girdle. The top ray of the upper lobe of the pectoral fin close to the level of the ventral margin of the eye. The dorsal and anal rays long and slender.

One snout pore; although two other pores are present on the snout and might be classified topographically with the snout series of Burke (1930, fig. 1), they are actually part of Burke's maxillary series. Maxillary pores seven, including one above and behind the eye and another below and behind the eye. Mandibular pores 7 (the anterior-most not shown in Fig. 1). Suprabranchial pores one. About a dozen rudimentary pores (see Burke, 1930:9 for a discussion of this character) are present above the midline along the anterior half of the body. They are small and difficult to discern and have been emphasized in Fig. 1. *P. calidus* and *P. wilsoni* (Richards, 1966) are the only known species of *Paraliparis* for which rudimentary pores have been recorded. These two species are not closely related, and I predict that rudimentary pores will be found in other species as adequate material becomes available.

The anus is close to a line between the lowest rays of the upper lobe of the pectoral fin. The body cavities of two paratypes are tightly packed with eggs of varying sizes, the largest 2.7 mm in diameter.

The head, fins, and belly are black; the skin on the body is paler and is punctulate with small black, densely distributed chromatophores.

Relationships.—*P. calidus* keys out to *P. bathybius* in Burke (1930), to which it seems closely related. It differs, however, in having the upper ~~lobe~~ rays of the pectoral fin and the opercular spine below a line through the center of the eye; in *P. bathybius* they are above such a line. In addition, *P. calidus* has higher counts (Table 2).

The bottom temperature at the type-

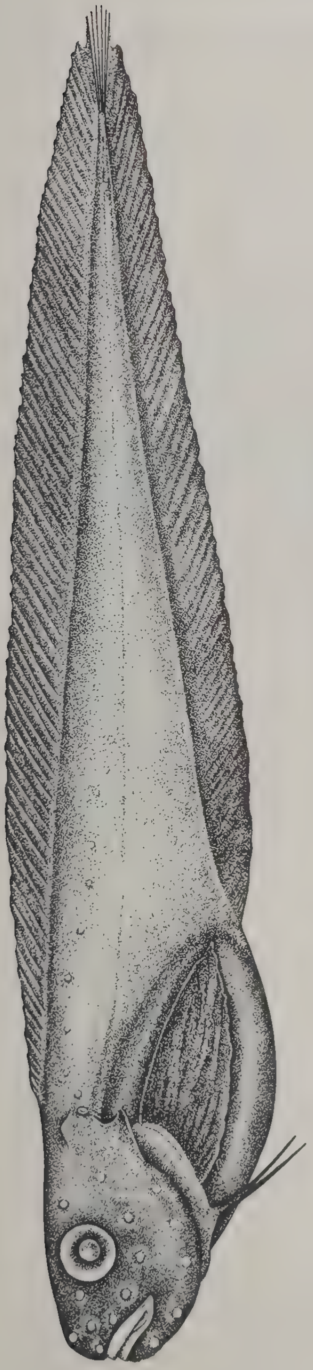

Fig. 1. *Paraliparis calidus.* Holotype, USNM 202469. Drawn by Mildred H. Carrington.

Table 2. Number of Fin Rays and Vertebrae of *Paraliparis calidus* and *P. bathybius*

		calidus	*bathybius*
Rays in upper lobe of pectoral fin[1]	11		3
	12		–
	13		2
	14		
	15	2	
	16	2	
	17	2	
	18	2	
Anal fin rays	50		1
	51		1
	52		–
	53		1
	54		–
	55		1
	56		
	57	1	
	58	2	
Free rays in dorsal fin	57		1
	58		1
	59		1
	60		1
	61		
	62	1	
	63	2	
Total vertebrae not including hypural	60		1
	61		–
	62		–
	63		1
	64		1
	65		–
	66		–
	67	1	1
	68	1	
	69	–	
	70	1	

[1] Counts made on both left and right pectorals in *P. calidus.*

locality of *P. calidus* was 6.2° C. *P. bathybius,* on the other hand, is a member of the Polar fauna of the Norwegian Sea and Davis Strait and is known only from waters with negative bottom temperatures (Jensen, 1905, 1950; Johnsen, 1919).

Name.—The word *calidus* is Latin for hot or warm, and refers to the higher temperature of the region where this species has been caught, compared with the home of its closest known relative.

Study material.—In addition to the types of *P. calidus* I have studied the holotypes of

G. edwardsi, Mus. Nat. Hist. Nat. Paris no. 86.522; and *Eutelichthys leptochirus*, Mus. Storia Nat. Genova no. 37691; three specimens of *Paraliparis leptochirus*, USNM 202474, Banyul, France; four specimens of *Paraliparis bathybius* in the Univ. Copenhagen Zool. Mus. (two from "Ingolf" station 119, and two from stations 105 and 111); and one specimen in the British Mus. Nat. Hist., no. 87.12.9.13.

ACKNOWLEDGMENTS

I thank M. L. Bauchot, P. H. Greenwood, J. Nielsen, and E. Tortonese for allowing me to examine specimens in their care. H. Bullis sent me the specimens of *P. calidus* and provided other information. Vu-Tan-Tue provided specimens of *P. leptochirus*. G. W. Wadley and E. Tortonese have read parts of the manuscript.

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DAECTOR SCHMITTI, A NEW SPECIES OF VENOMOUS TOADFISH FROM THE PACIFIC COAST OF CENTRAL AMERICA

By Bruce B. Collette

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In my recent review (Collette, 1966) of the venomous toadfishes (Batrachoididae, Thalassophryninae), I tentatively referred to a specimen from Costa Rica as a variant of *Daector reticulata* (Günther) although I believed that it might represent an undescribed species. I did not describe it because I had only the single specimen, which closely resembled *D. reticulata* in color pattern. A second, larger, specimen, from Panama has come to my attention and I am now convinced that these two fish represent an undescribed species. I take great pleasure in naming the new species in honor of the energetic collector of the holotype—Dr. Waldo L. Schmitt.

Daector schmitti new species
(Fig. 1)

Diagnosis: A species of *Daector* most similar to *D. reticulata* but differing in having fewer second dorsal rays (22 vs. 25–27); anal rays (21 vs. 24–26); and caudal vertebrae (23 vs. 26–28). The filaments on the head of *D. schmitti* extend farther laterally than in *D. reticulata*—beyond the infraorbital lateral line canal, instead of to the canal. *D. schmitti* has a color pattern similar to that of the smaller sizes (80 mm) of *D. reticulata* but loses the reticulations and develops a spotted pattern reminiscent of the Atlantic species *Thalassophryne maculosa* Günther at larger sizes (130 mm). Precaudal vertebrae 8. Pectoral fin glands 6.

Comparisons: D. schmitti has a much more extensive distribution of filaments on the head and anterior part of the body than does *D. reticulata* although the filaments are larger in *D. reticulata* (Fig. 2). Filaments cover a greater area in larger specimens of both species. They extend farther laterally in *D. schmitti*—below the infraorbital canal on

Table 1.—Morphometric comparison of *Daector schmitti* with *D. reticulata* (in percentage of standard length).

	D. reticulata		*D. schmitti*		*D. reticulata*		
	USNM 81697	SU 22287	SU 14949	USNM 144869	SU 22287	USNM 81698	SU 22287
Standard length (mm)	52.7	53.8	80.1	130	167	185	193
Head length	31.3	32.0	36.0	36.8	30.5	29.8	32.0
Head width	28.8	30.1	34.5	38.1	32.2	29.4	30.1
Interorbital distance	4.7	4.3	7.1	7.7	6.9	6.1	6.0
Snout–1 dorsal	29.2	26.2	29.0	34.1	28.2	26.6	29.7
Snout–2 dorsal	39.3	37.7	43.9	46.4	44.6	40.9	44.2
2nd dorsal base	55.6	56.1	52.4	56.5	52.4	60.5	57.5
Snout–anal	42.5	42.0	49.9	53.1	45.6	46.4	45.0
Anal base	55.6	56.9	53.7	56.7	54.3	58.1	54.9
Snout–pectoral	30.6	29.9	36.7	37.1	30.7	31.1	31.5
Pectoral length	27.5	29.7	27.2	29.1	25.0	24.2	25.2
Snout–pelvic	18.8	19.7	22.1	23.5	19.5	19.6	19.5
Pelvic length	18.0	17.1	20.0	18.9	17.5	16.2	16.6

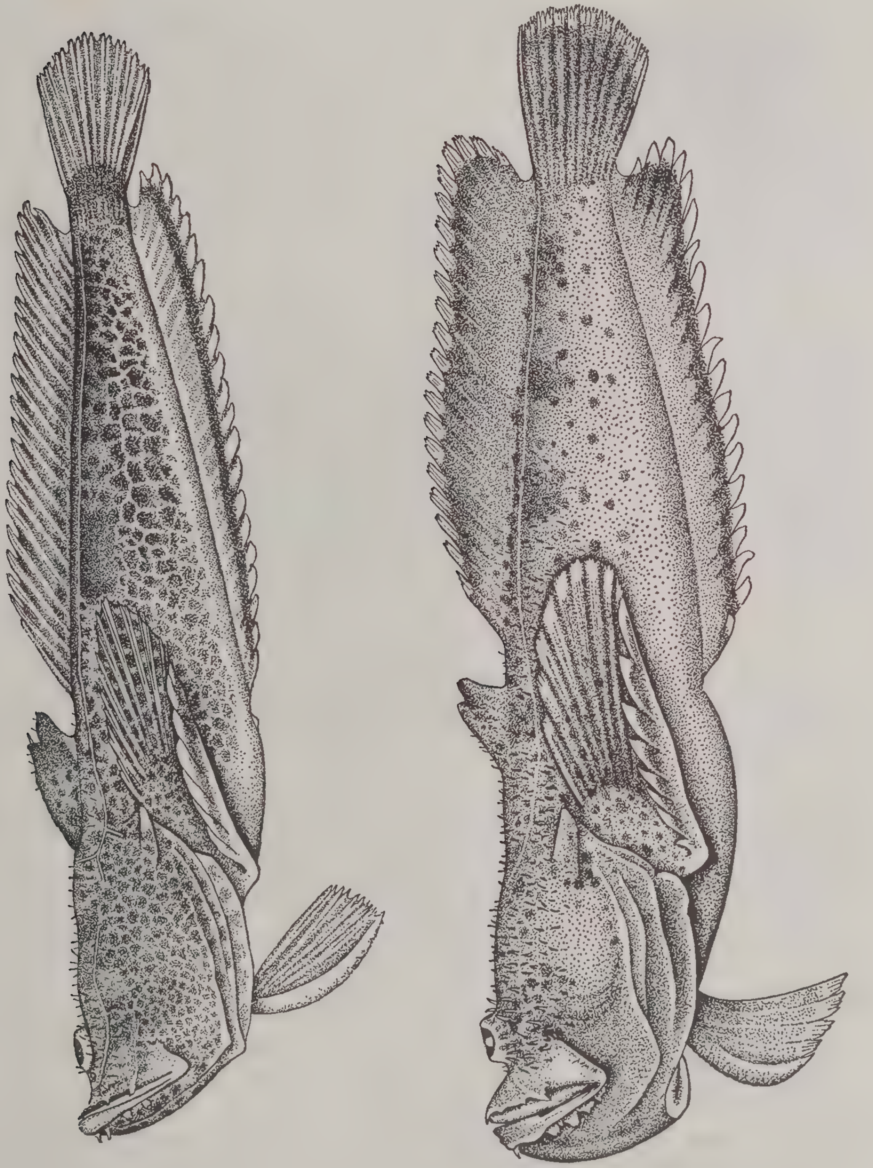

Fig. 1. *Daector schmitti.* Left, SU 14949, paratype, 80.1 mm SL, Golfo de Nicoya, Costa Rica. Right, USNM 144869, holotype, 130 mm SL, Secas Islands, Panama.

the head, and below the lateral line on the body in the region of the second dorsal fin origin. In *D. schmitti,* the filaments cover much of the membrane over the dorsal spines and extend posteriorly as far as the eighth ray in the second dorsal fin. In eight large (185–252 mm SL)

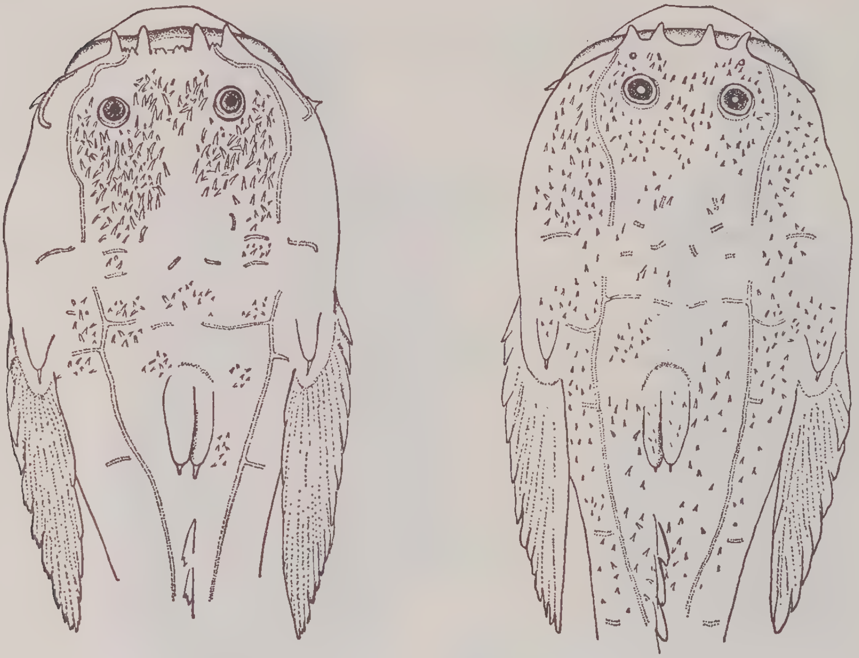

Fig. 2. Dorsal view of heads of *Daector reticulata* (left, USNM 81698) and *D. schmitti* (right, USNM 144869) showing distribution of filaments.

specimens of *D. reticulata,* the filaments extend posteriorly no farther than the second or third ray in the second dorsal fin.

D. schmitti agrees with both *D. reticulata* and *D. gerringi* (Rendahl) in having one fewer ray in the second dorsal fin than the number of caudal vertebrae. *D. dowi* (Jordan and Gilbert) has the same number of second dorsal fin rays as caudal vertebrae.

Morphometrically, *D. schmitti* has a longer, wider head, greater interorbital distance, longer pelvic fins, and greater snout–pectoral and snout–pelvic distance than does *D. reticulata* (Table 1).

Types: Holotype—U. S. Nat. Mus. 144869, 130 mm standard length; Panama, Secas Islands, from channels in coral tidal flat; 6 February 1935; VELERO 434–35. *Paratype*—Stanford Univ. 14949, 80.4 mm; Costa Rica, Golfo de Nicoya, Negritos Island, tidepools; 13 February 1947; M. B. Schaefer.

Discussion: The low number of caudal vertebrae and anal and second dorsal rays tend to bridge the gap between *Daector* which has high counts and *Thalassophryne* which has low counts. *D. schmitti,* however, agrees with *D. reticulata, D. gerringi,* and *D. dowi* in the three diagnostic characters of the genus: possession of discrete pectoral fin glands (see Fig. 1 in Collette, 1966), 8 precaudal vertebrae instead of 7, and a submarginal stripe in either the second dorsal or anal fin or both.

Dr. William A. Bussing, University of Costa Rica, has informed me that he has not found any toadfishes in the many tidal pool and inshore rotenone collections made between Bahía Culebra and Punta Mala. He suggests that *D. schmitti* may be restricted to island shores.

Acknowledgments: I am grateful to Mr. Robert E. Trist, Division of Fishes, U. S. National Museum, for calling the holotype to my attention and to Dr. Warren C. Freihofer, Stanford University, for lending me the paratype of *D. schmitti*. The figures were drawn by Mrs. Mildred H. Carrington. Drs. Daniel M. Cohen and Victor G. Springer have commented on the manuscript.

Addendum: After this manuscript was sent to the printer, Mr. Robert J. Lavenberg of the Los Angeles County Museum discovered a third specimen of *D. schmitti*: LACM 22360, 20.0 mm SL; Costa Rica, Port Culebra, off South Viradore Islands, 10°35′N, 85°43′W; 10 fms. over sand and shells; 25 February 1934; VELERO 257–34. It agrees exactly with the other two types in counts: D II, 22; A 21; vertebrae $8 + 23 = 31$. Like the holotype, this paratype was also collected by Dr. Schmitt from an island while on one of the *Velero III* expeditions (Fraser, 1943a, 1943b).

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pp. 189–192

STRONGYLURA TIMUCU (WALBAUM): A VALID SPECIES OF WESTERN ATLANTIC NEEDLEFISH.—Recent workers (Berry and Rivas, 1962; Mees, 1962; Collette and Berry, 1965) have recognized only two species of *Strongylura* in the western Atlantic: *Strongylura marina* (Walbaum) [= *Belone houttuyni* (Walbaum) according to Mees] and *Strongylura notata* (Poey) [= *Belone notata* according to Mees] and have considered *S. timucu* (Walbaum) a synonym of *S. marina*. This paper clearly demon-

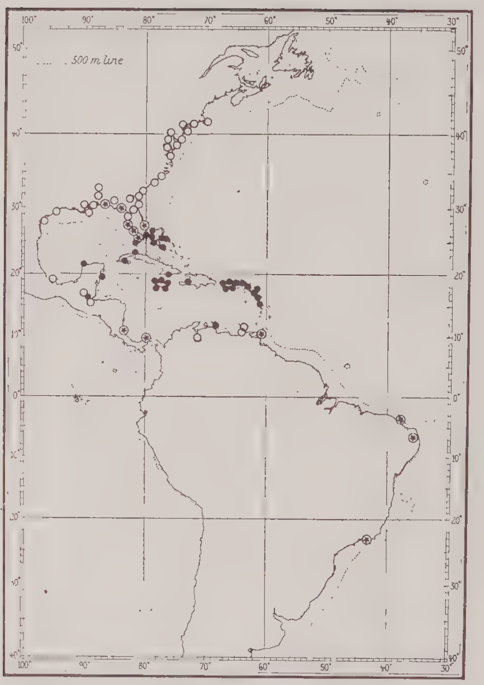

Fig. 1. Distribution (based on specimens examined) of *Strongylura marina* (open circles) and *S. timucu* (dots). Stars indicate sympatry.

strates that *S. timucu* (Walbaum) is a third valid western Atlantic species. More complete data on *S. timucu* and the other western Atlantic species of needlefishes will be published in a forthcoming volume of "Fishes of the Western North Atlantic."

S. notata differs from *S. marina* and *S. timucu* in having the maxillary entirely concealed under the preorbital bone instead of being exposed posteriorly, in having fewer anal rays (13–15 vs. 16–20), fewer vertebrae (55–60 vs. 66–76), and fewer predorsal scales (84–117 vs. 120–304).

S. timucu differs from *S. marina* in two major characters: 1) Both left and right gonads are developed instead of only the right one; 2) there are fewer predorsal scales, 120–185 ($\bar{x}$ 156, N 254) vs. 213–304 ($\bar{x}$ 256, N 145). Typically, *S. timucu* is darker than *S. marina*. Melanophores usually extend to the ventral margin of the orbit in *S. timucu* but not past the middle of the orbit in *S. marina*; the preorbital bone is densely pigmented in *S. timucu* and slightly in *S. marina*; the melanophores are present along the lateral line in *S. timucu* but usually absent in *S. marina*. From time–share computer-plotted scattergrams and analysis of slopes and heights of regression lines, I found that *S. marina* and *S. timucu* differ significantly (values greater than for F .999) in 8 of 11 morphometric characters. The most obvious difference is in interorbital width where *S. timucu* has a greater distance ($Y = .0566x - .6716$ for *timucu*, $Y = .0510x - .5862$ for *marina*, F for heights = 65.1).

These two species are sympatric in much of the western Atlantic, although only *S. marina* occurs on the Atlantic coast north of Florida and in the western Gulf of Mexico, and only *S. timucu* occurs in the Antilles and Bahamas (Fig. 1). *S. marina* extends from Maine south to mid-peninsula Florida, across the Gulf Coast of the United States and Mexico and along the coasts of Central and South America at least to Rio de Janeiro, Brazil. *S. timucu* ranges from Jupiter Inlet on the east coast and Pensacola on the panhandle of Florida south through the Florida Keys, Bahamas, and Antilles. It also occurs along the coasts of Central and South America from Yucatan at least to Rio de Janeiro.

Aside from identification and distribution, *S. marina* and *S. timucu* offer nomenclatorial problems. As pointed out previously (Collette and Berry, 1965, 1966), the name *Strongylura marina* (Walbaum, 1792) has been consistently used for this common western Atlantic *Strongylura* and should be used instead of *Esox houttuyni* Walbaum, 1792 which was used by Mees (1962, 1964) in spite of its being a *nomen oblitum.*

The problem of the proper name for *S. timucu* is more complex. At least 14 names have been proposed which apply to one or the other of the two species under discussion. The earliest three were all proposed by Walbaum in 1792. *Esox marinus* was based on a specimen from New York, so it is certain that it is the species presently known as *S. marina,* because it is the only species of *Strongylura* occurring that far north. Mees (1962) selected the name *Esox houttuyni* for this species and noted that "Houttuyn's description is a good one for the species, and with the knowledge that his specimen came from the American waters, there is no reason at all for doubt." Thus, the name *houttuyni* could be based on a specimen of either *marina* or *timucu.* The third Walbaum name, *Esox timucu,* was based on Marcgrave (1648) and as Mees (1962:73) noted, neither the figure nor the description in Marcgrave is very helpful. Both species of *Strongylura* occur in Brazil so Marcgrave's type-locality offers no help. Because the name *timucu* has frequently been used for this species (Jordan and Evermann, 1896:711; Meek and Hildebrand, 1923:229; Longley and Hildebrand, 1941:28; Breder, 1948:88; etc.), I believe it is necessary to designate a neotype for *Esox timucu* Walbaum in order to stabilize the name for the species. Since the name *timucu* was based only on a figure, no type-specimens are extant. Brazilian specimens of *S. timucu* are available in the Stanford University collections.

Strongylura timucu (Walbaum)

Esox timucu Walbaum, 1792:88—Brazil (based on Marcgrave, 1648:168).

Belone cigonella Valenciennes *in* Cuvier and Valenciennes, 1846:323—Porto Rico. No type-specimens extant.

Belone subtruncata Poey, 1860:295—Havana, Cuba. No type-specimens extant.

Belone depressa Poey, 1860:296—Havana, Cuba. Holotype, U. S. Nat. Mus. 4745.

Belone diplotaenia Cope, 1871:481—St. Martin, West Indies. Holotype, Acad. Nat. Sci. Phila. 7572.

Tylosurus sagitta Jordan and Gilbert, 1884: 25—Key West, Florida. Lectotype, herein selected, U. S. Nat. Mus. 34965.

Tylosurus euryops Bean and Dresel, 1884: 168—Jamaica. Holotype, U. S. Nat. Mus. 32073.

Neotype.—Stanford Univ. 22073, ♀ 219 mm body length, 342 mm standard length. Brazil, Lake Papary, about 24 miles south of Natal; E. C. Starks; 1911. Meristic characters: predorsal scales 148; gonads two, left 69 mm, right 89 mm; dorsal rays 17; anal rays 19; pectoral rays 10 on each side. Morphometric characters (in mm): head length 123; snout length 81.7; lower jaw extension 4.0; postorbit length 31.5; preopercle length 18.3; orbit length 11.3; interorbital width 12.7; head depth at posterior margin of orbit 17.7; head width 15.5; pectoral fin length 32.9; pelvic fin length 16.4.

Three other specimens of *S. timucu* (84–239 mm BL), recatalogued as SU 64919 and four specimens of *S. marina* (106–329 mm BL), recatalogued as SU 64920, were in the same jar with the neotype. These fish were all reported by Starks (1913) as *Tylosurus almeida* (Quoy and Gaimard).

I considered the possibility of using for the species one of the other six names here placed in the synonymy of *S. timucu*. However, the junior synonyms based on West Indian specimens (*cigonella, subtruncata, depressa, diplotaenia, euryops*) and on Key West specimens (*sagitta*) have had little usage in the literature; therefore, stability seems best served by designating a neotype for the earliest name, *timucu*, and employing that name.

F. H. Berry, J. E. Böhlke, R. H. Gibbs, Jr., J. E. Randall, and V. G. Springer have read and commented on drafts of this note.

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ologiae proponitur cum classibus, ordinibus, generum characteribus, specierum differentiis, observationibus plurimis. Ichthyologiae. Pars III. Grypeswaldie.

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A Comparison of Current and Long-Term Temperatures of Continental Shelf Waters, Nova Scotia to Long Island

BY JOHN B. COLTON, JR.

Abstract

Offshore temperature conditions during December 1964 and 1965, March 1953, 1965, and 1966, and May–June and September 1965 and 1966 are compared with 1940–59 mean values for these months. Charts showing the distribution of temperature at the surface, 20 m, 50 m, and 100 m, and of temperature anomalies at the surface, 20 m, and 50 m are presented. At most locations and depths the 1964-66 temperatures were appreciably colder than the 1940-59 mean values. The magnitude of the negative anomalies tended to be greatest in areas off the edge of the Continental Shelf. Temperatures in March 1953 were warmer than the 1940–59 mean values. These trends paralleled trends at coastal stations as exemplified by Boothbay Harbor, Maine temperatures. The reliability of the use of coastal temperatures for indexing offshore conditions, the possible biological effects of warming and cooling trends, and the causes of these trends are discussed.

Introduction

This paper provides a summary of current and long-term temperature conditions during March, May–June, September, and December in the Continental Shelf area bounded by longitudes 64°W and 72°W. The long-term temperature data are for 1940–59, and are from the file of bathythermograph and oceanographic station observations at the Woods Hole Oceanographic Institution. The current temperature data were collected on a series of eight quarterly environmental surveys made by the U.S. Bureau of Commercial Fisheries from December 1964 to September 1966. These surveys, conducted during a period of severe drought in the New England area, afford an opportunity to compare recent inshore and offshore temperatures with long-term means.

Analysis of the Data

The initial monthly tabulation of the 1940–59 temperature data was made on a basis of 10-min quadrangles at depths of 1, 10, 20, 30, 40, 50, 75, 100, 150, 200, and 250 m. In this report these data have been grouped in terms of 30-min quadrangles.

Observations for any month within a given year were weighted in favor of certain days (dates). To offset possible bias in determining monthly means all data for a given day were averaged and monthly means based on the daily means rather than on the total number of observations. Some of the inshore quadrangles included daily observations made at lightships. To eliminate the bias of the data in these quadrangles due to the preponderance of lightship observations, 10-day mean values of lightship observations were determined for each month and these values treated as three observations.

Because observations were so few in certain months, the 1940–59 monthly mean values at specific depths were plotted and smooth curves showing the seasonal cycle of temperature were drawn as described by Fuglister (1947). In drawing these curves the greatest weight was given to mean values for months having the most years represented. The resultant curves for specific depths in adjacent quadrangles were so closely similar that occasional inconsistencies in the data were obvious. A sample of seasonal temperature curves and the corrections applied at the surface, 50 m, and 100 m is shown in Fig. 1. The correction applied to monthly mean values based on a small number of observations was often considerable; where only a few years were represented the corrected value was sometimes outside the range of the observed temperatures.

All 1940–59 mean temperature values were read from these seasonal curves and isotherms were drawn on a basis of corrected values entered at the center of each 30-min quadrangle. The May–June mean temperature values for 1940–59 are based on an average of the corrected values for these 2 months. Temperature distributions based

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[1]Bureau of Commercial Fisheries Biological Laboratory, Woods Hole, Massachusetts, USA.

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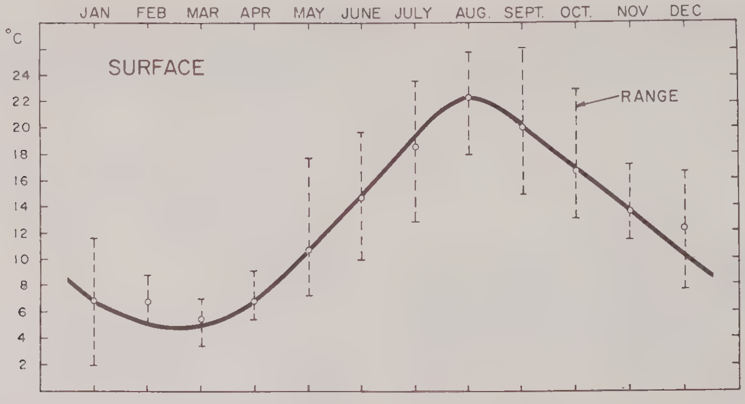
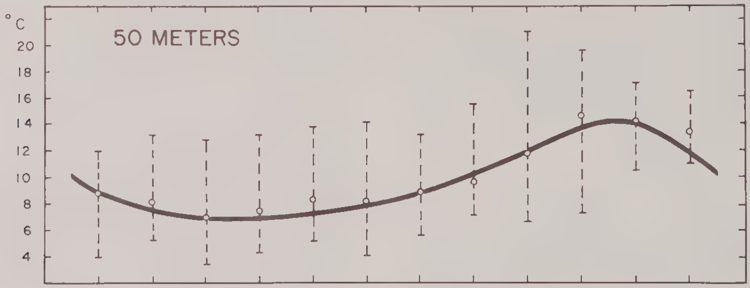
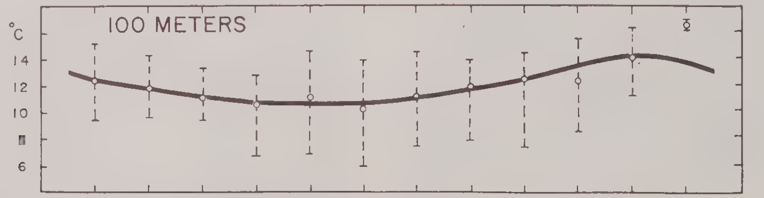


NO OF OBSERVATIONS	37	11	22	20	54	105	114	97	127	48	37	16
NO OF DAYS	11	9	7	12	14	25	28	26	35	20	9	4
NO OF YEARS	7	5	5	6	9	11	11	13	14	11	6	3
AVERAGE TEMP.	6.9	6.8	5.5	6.8	10.7	14.7	18.5	22.3	20.0	16.7	137	12.4
CORRECTED TEMP.		52	5.0				19.2			16.8		10.4



NO. OF OBSERVATIONS	35	10	22	18	53	95	107	97	125	40	36	14
NO. OF DAYS	9	8	7	11	14	24	25	26	34	17	9	4
NO. OF YEARS	6	5	5	7	9	11	9	13	13	9	6	3
AVERAGE TEMP.	8.8	8.2	7.0	7.5	8.4	8.2	8.9	9.7	11.8	14.7	14.3	13.5
CORRECTED TEMP.		7.6		7.0	7.4	8.0		10.4	12.0	13.9		11.8



NO. OF OBSERVATIONS	24	4	19	10	43	60	69	57	68	25	18	7
NO. OF DAYS	7	4	7	5	12	18	19	17	24	14	6	2
NO. OF YEARS	6	4	5	5	9	9	7	8	12	9	4	1
AVERAGE TEMP.	12.3	11.7	11.0	10.5	11.0	101	110	118	12.3	12.2	139	164
CORRECTED TEMP.		11.6			10.5	10.6		11.7		13.3	14.0	13.6

Fig. 1. Seasonal temperature curves and temperature corrections applied for 30-min quadrangle, 40°00′N to 40°29′N, 70°30′W to 70°59′W.

on the quarterly environmental survey data were determined from *in situ* bathythermograph observations.

Accuracy of the Data

The greatest single source of error in the 1940–59 mean temperature data was faulty navigation. Position errors were not always easy to detect, but in relatively shoal water (<250 m) a comparison of the bathythermograph echo sounder depth with chart soundings usually would reveal the error. Errors due to defective instruments were relatively few and these were usually detected easily. A considerable amount of personal judgment was involved in deciding what observations were in error; generally this decision was withheld until a comparison could be made with supplementary observations.

Validity of the Data

Iselin (1955) has discussed the complications of obtaining a synoptic picture of the distribution of physical and chemical properties in coastal waters characterized by strong tidal and nontidal currents and short-period internal waves. Obviously when observations are averaged for an area as large as a 30-min quadrangle for a period as long as a month, only the most general approximation of reality is obtained. This fact is evidenced by the appreciable ranges in monthly temperature values observed in most quadrangles and at most depths and by the greater sharpness of horizontal and vertical gradients based on quarterly environmental survey data compared with those based on 1940–59 mean data. The validity of the temperature estimates based on monthly mean values varies with the season. These estimates are nearest actual conditions in the winter, when temperature gradients are weak over most of the area. Summer on the other hand, is a period of strong horizontal and vertical stratification.

Examples of short-term temperature fluctuations at anchor and parachute drogue stations and at "repeat" sections in the Gulf of Maine-Georges Bank area during the summer are shown in Fig. 2. The variations in temperature observed in a specific water mass and at specific locations were considerable; it is apparent that internal waves as well as advection were a contributing factor. Although the methods used impose serious limitations, whereby temperature values based on long-term averages are employed to interpret conditions in a region characterized by large temporal and spatial fluctuations, the method does appear to provide a general picture of the major temperature features to which specific cruise data may be compared.

Distribution of Temperature

The distribution of temperature during March, May–June, September, and December at the surface, 20 m, 50 m, and 100 m, based on 1940–59 mean values and 1964, 1965, and 1966 quarterly environmental survey data is shown in Fig. 3–10.

In general, the 20-year mean and specific year seasonal and areal temperature trends at all depths were similar; minimum temperatures occurred in March and inshore and maximum temperatures occurred in September and offshore. As would be expected, the temperature gradients based on survey cruise data were much sharper than those based on 1940–59 mean values. The contrast in the complexity of the distribution patterns based on 1940–59 mean and survey cruise data was greatest in September. The most striking feature of the data is that with but few exceptions the survey cruise temperatures were lower than the 1940–59 mean temperatures during all months and at all depths and locations.

Temperature Anomalies

To assess current temperature trends more effectively, temperature anomalies were computed as the difference between the monthly mean for a specific year and the monthly mean for the base period 1940–59. In determining 1940-59 means, 30-min quadrangle values within 1- or 1/2-degree quadrangles were averaged. Monthly means for specific years were determined by averaging all station data within 1- or 1/2-degree quadrangles. Values from survey cruise stations located on whole degree latitude or longitude lines were entered in the quadrangle immediately to the south or west. Monthly temperature anomalies at the surface, 20 m and 50 m for specific years are shown in Fig. 11–14.

With the exception of surface values along the New England coast during May–June 1965 and 1966, 20-m values in the Wilkinson Basin area in September 1965, and surface and 20-m values in the central and western Gulf of Maine and off the southwest coast of Nova Scotia in

September 1966, all temperature anomaly values were negative. Although not illustrated, all 100-m anomalies were negative with the exception of positive values at the extreme southeasterly quadrangle during May–June 1965 and 1966. Considering that at most locations and seasons the temperature data from survey cruises were characterized by marked short-term fluctuations and that the temperature data for any quadrangle represent a sampling period of less than 12 hr, the temperature anomalies are remarkably consistent.

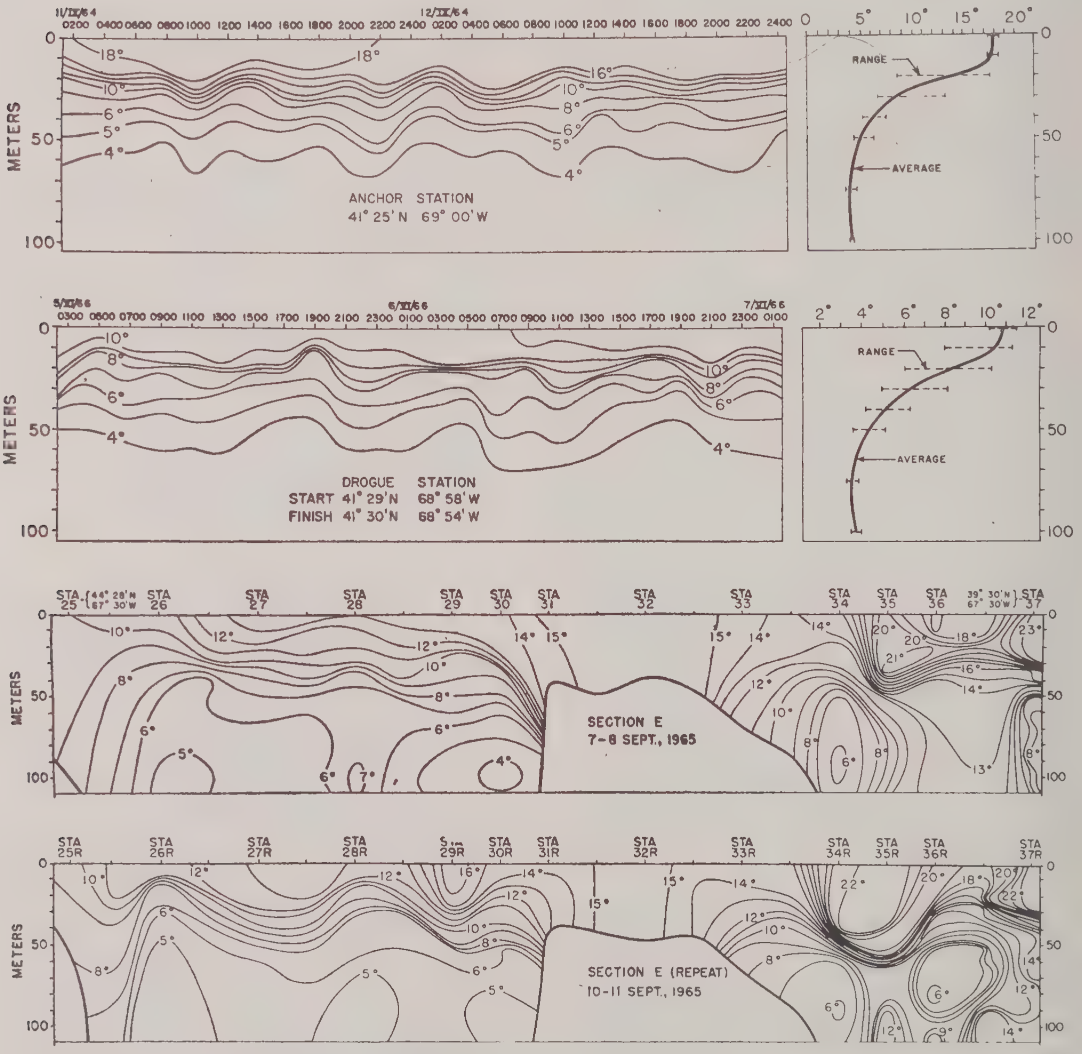


Fig. 2. Temporal variations in the distribution of temperature at anchor and frogue stations and at repeat sections.

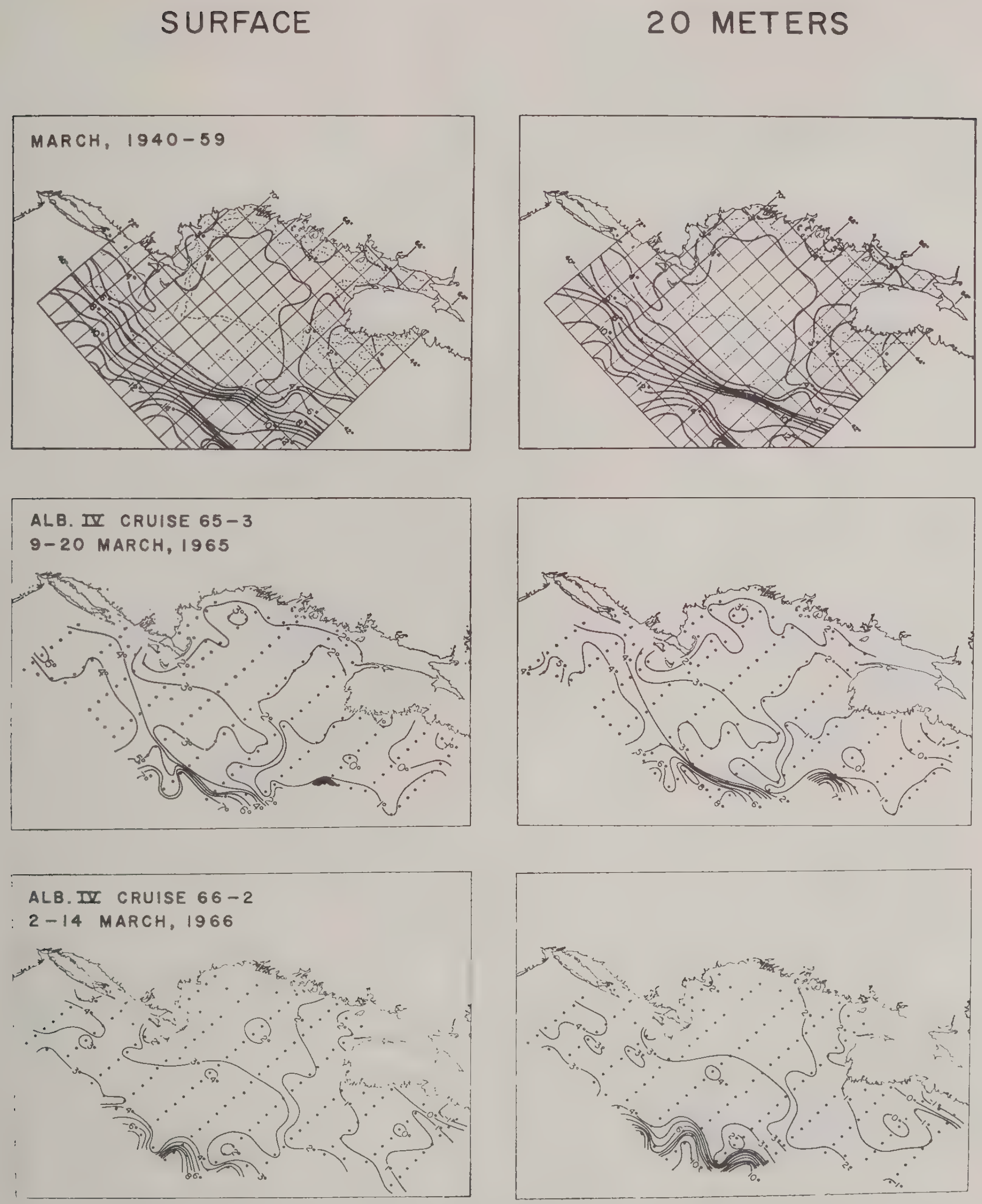

SURFACE
20 METERS
MARCH, 1940–59
ALB. IV CRUISE 65–3
9–20 MARCH, 1965
ALB. IV CRUISE 66–2
2–14 MARCH, 1966

Fig. 3. Temperature distribution at the surface and 20 m, March 1940–59, 1965, and 1966.

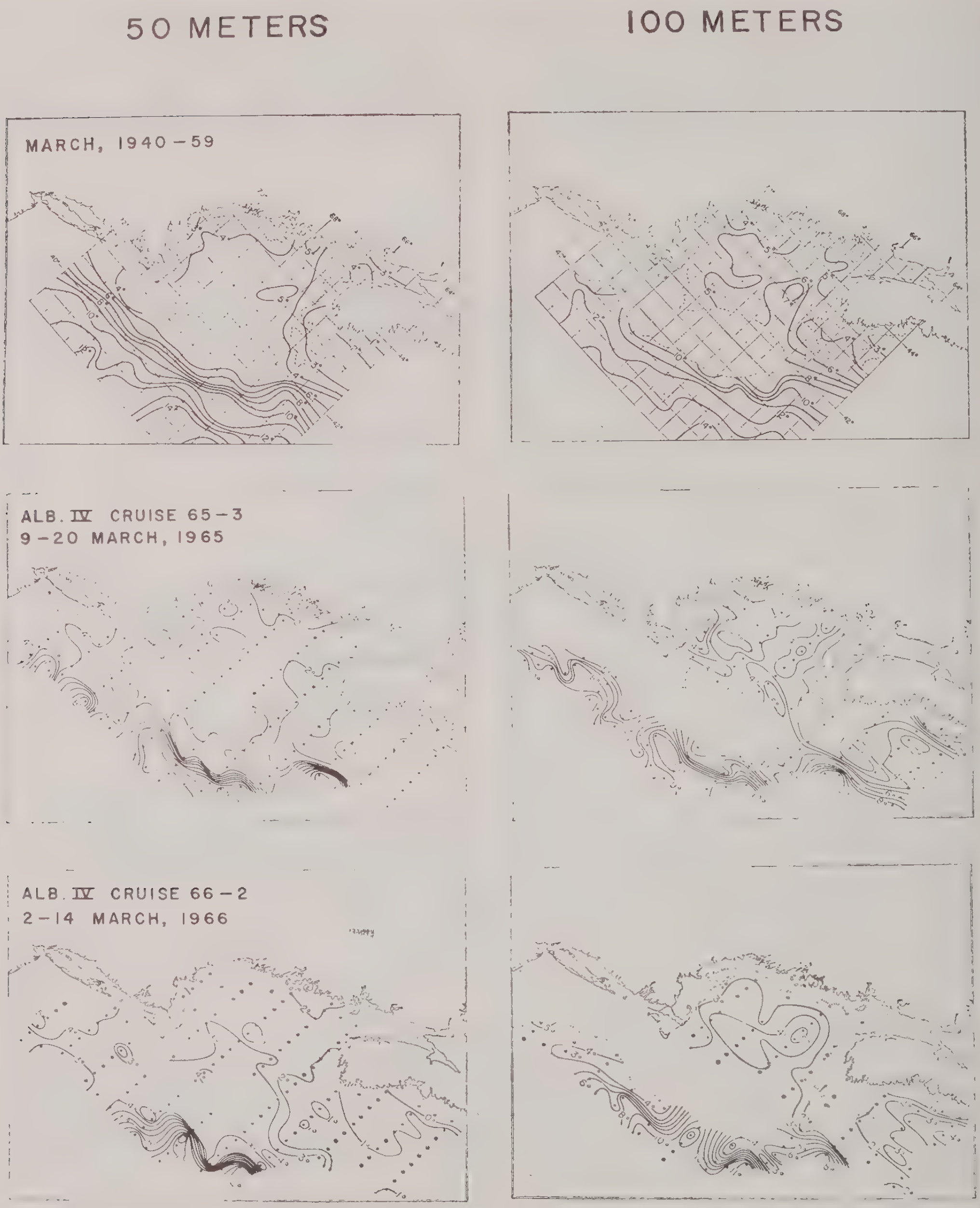

50 METERS
100 METERS
MARCH, 1940 — 59
ALB. IV CRUISE 65 — 3
9 — 20 MARCH, 1965
ALB. IV CRUISE 66 — 2
2 — 14 MARCH, 1966

Fig. 4. Temperature distribution at 50 and 100 m, March 1940–59, 1965, and 1966.

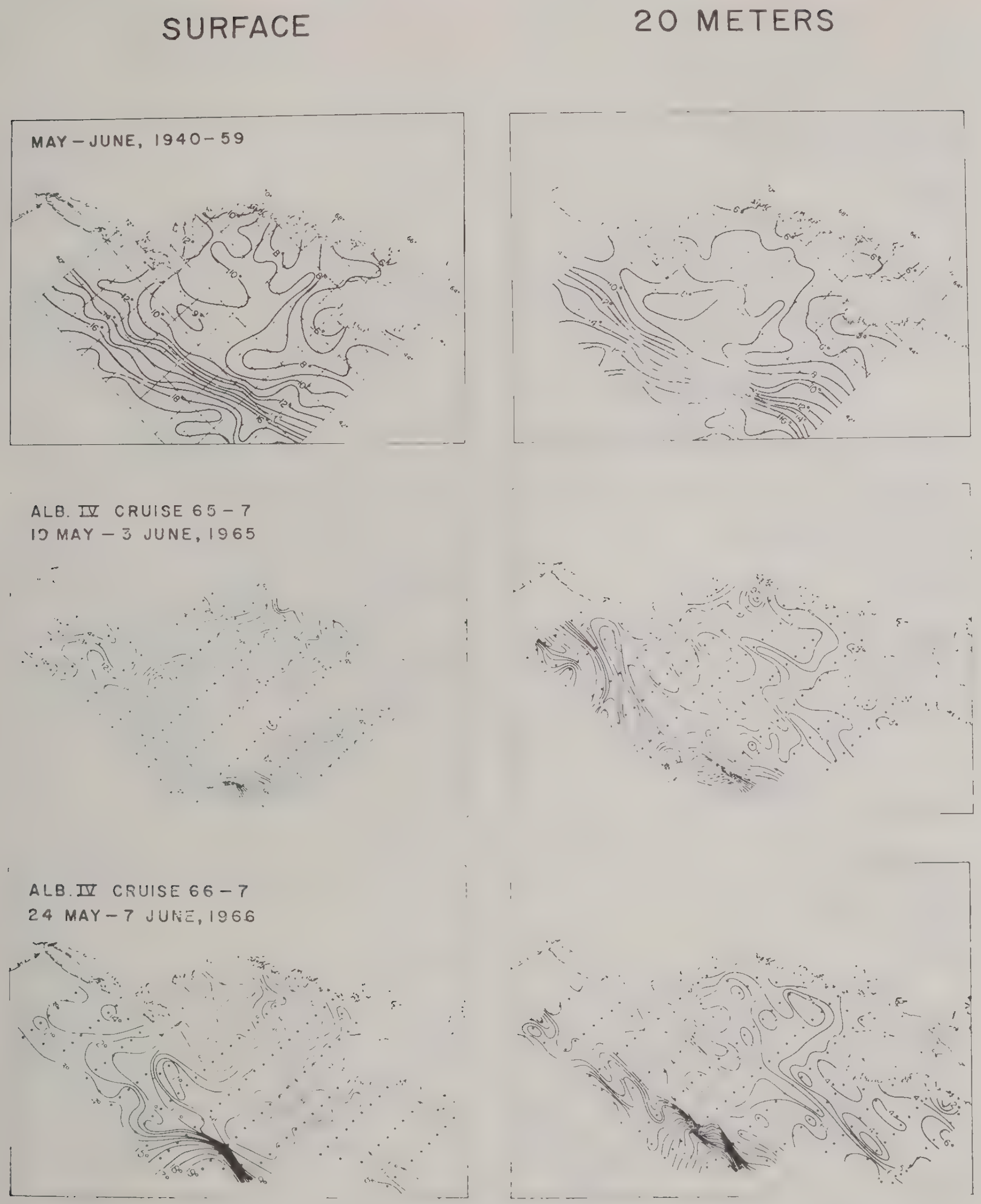

SURFACE
20 METERS
MAY – JUNE, 1940 – 59
ALB. IV CRUISE 65 – 7
10 MAY – 3 JUNE, 1965
ALB. IV CRUISE 66 – 7
24 MAY – 7 JUNE, 1966

Fig. 5. Temperature distribution at the surface and 20 m, May–June 1940–59, 1965, and 1966.

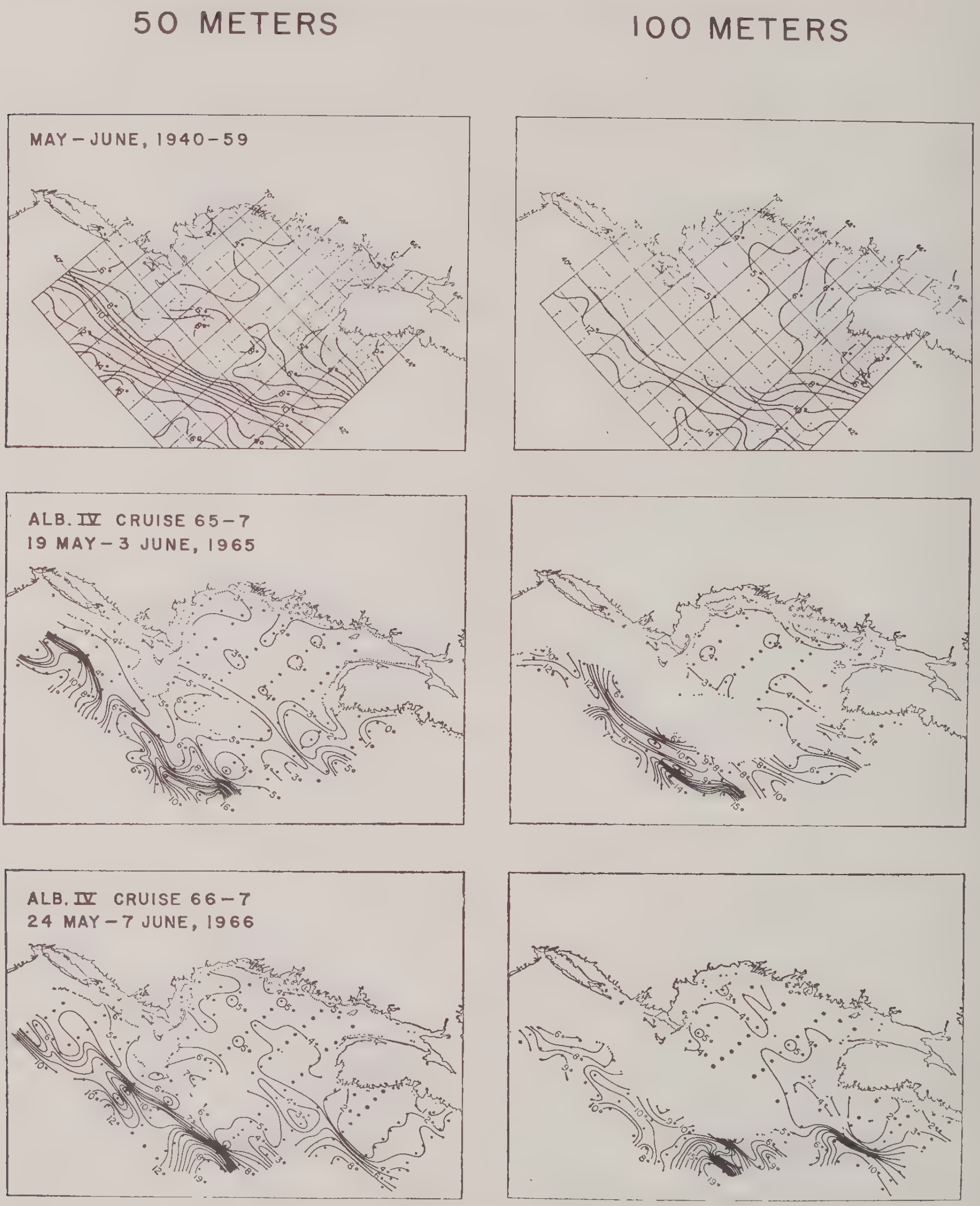

50 METERS
100 METERS
MAY – JUNE, 1940–59
ALB. IV CRUISE 65–7
19 MAY – 3 JUNE, 1965
ALB. IV CRUISE 66–7
24 MAY – 7 JUNE, 1966

Fig. 6. Temperature distribution at 50 and 100 m, May–June 1940–59, 1965, and 1966.

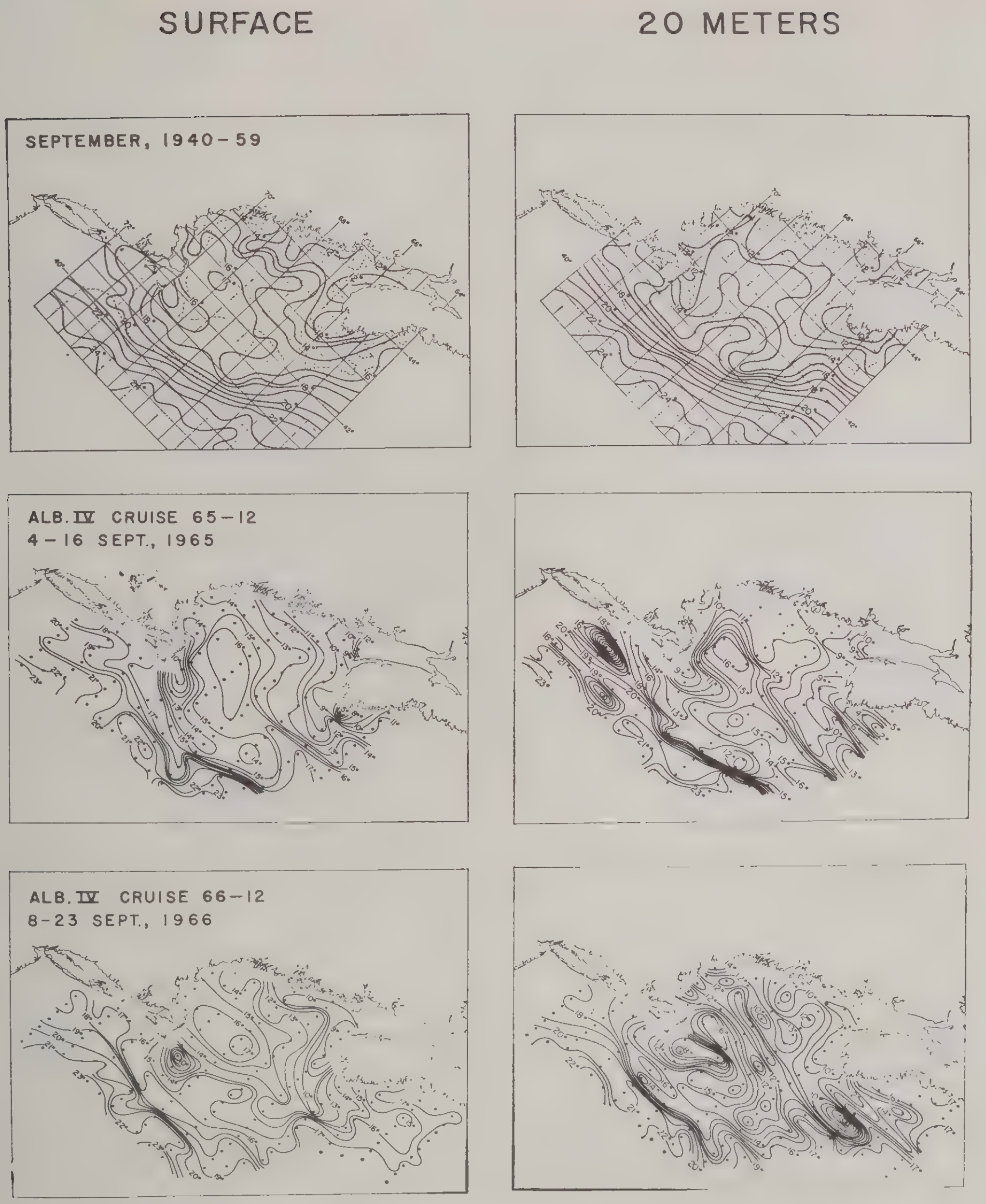

SURFACE
20 METERS
SEPTEMBER, 1940-59
ALB. IV CRUISE 65-12
4-16 SEPT., 1965
ALB. IV CRUISE 66-12
8-23 SEPT., 1966

Fig. 7. Temperature distribution at the surface and 20 m, September 1940–59, 1965, and 1966.

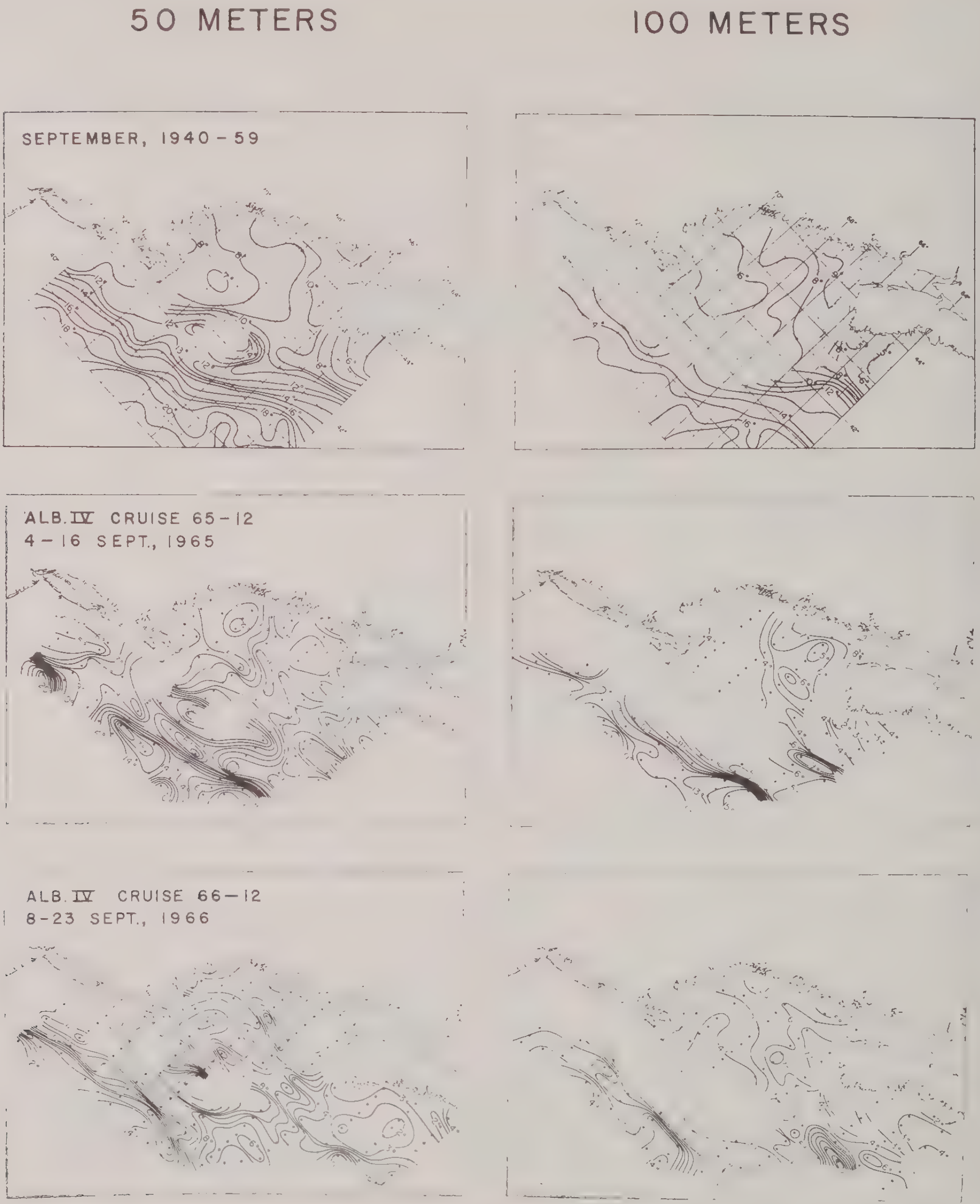

50 METERS
100 METERS
SEPTEMBER, 1940 – 59
ALB. IV CRUISE 65 – 12
4 – 16 SEPT., 1965
ALB. IV CRUISE 66 – 12
8 – 23 SEPT., 1966

Fig. 8. Temperature distribution at 50 and 100 m, September 1940–59, 1965, and 1966.

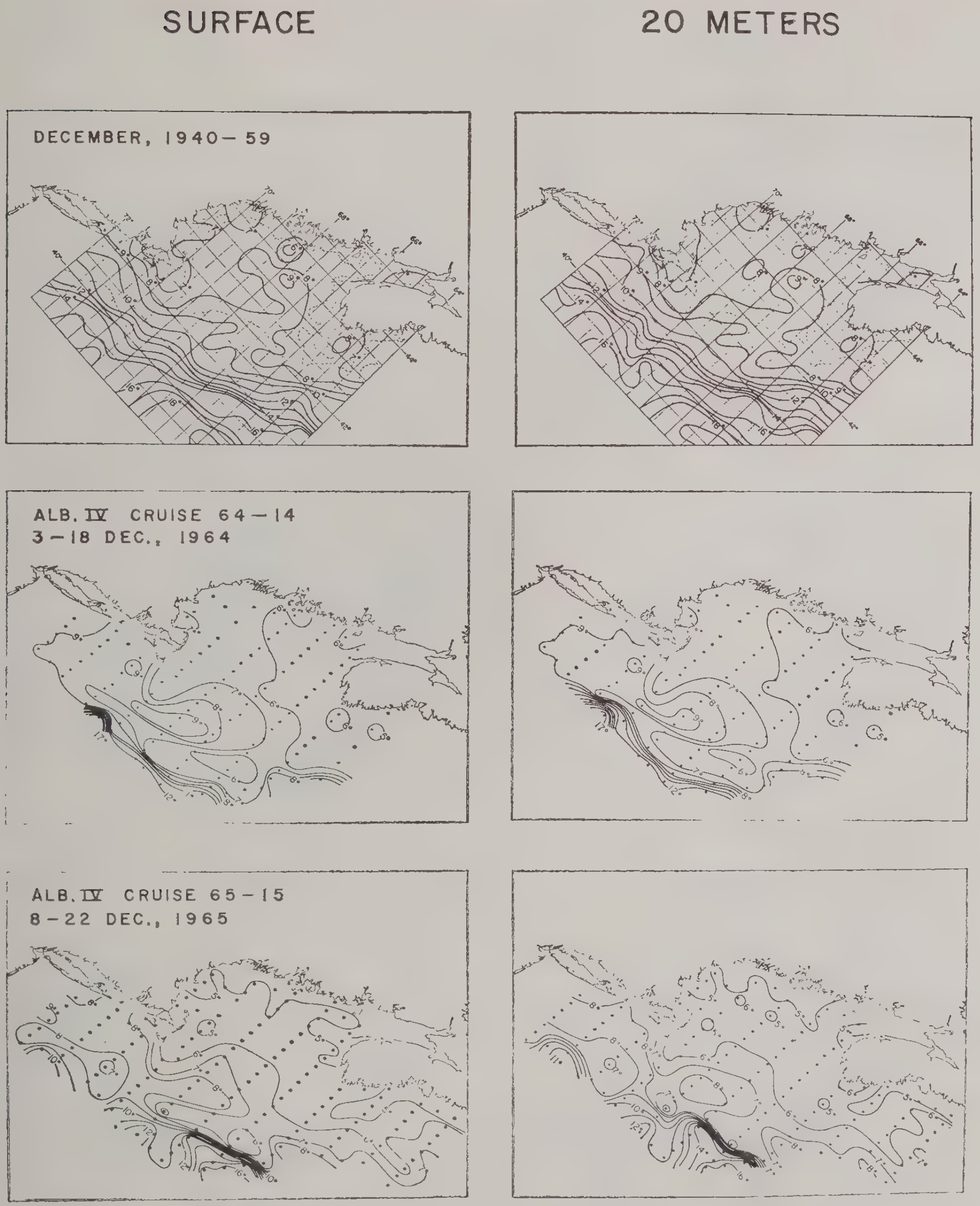

SURFACE
20 METERS
DECEMBER, 1940—59
ALB. IV CRUISE 64—14
3—18 DEC., 1964
ALB. IV CRUISE 65—15
8—22 DEC., 1965

Fig. 9. Temperature distribution at the surface and 20 m, December 1940–59, 1964, and 1965.

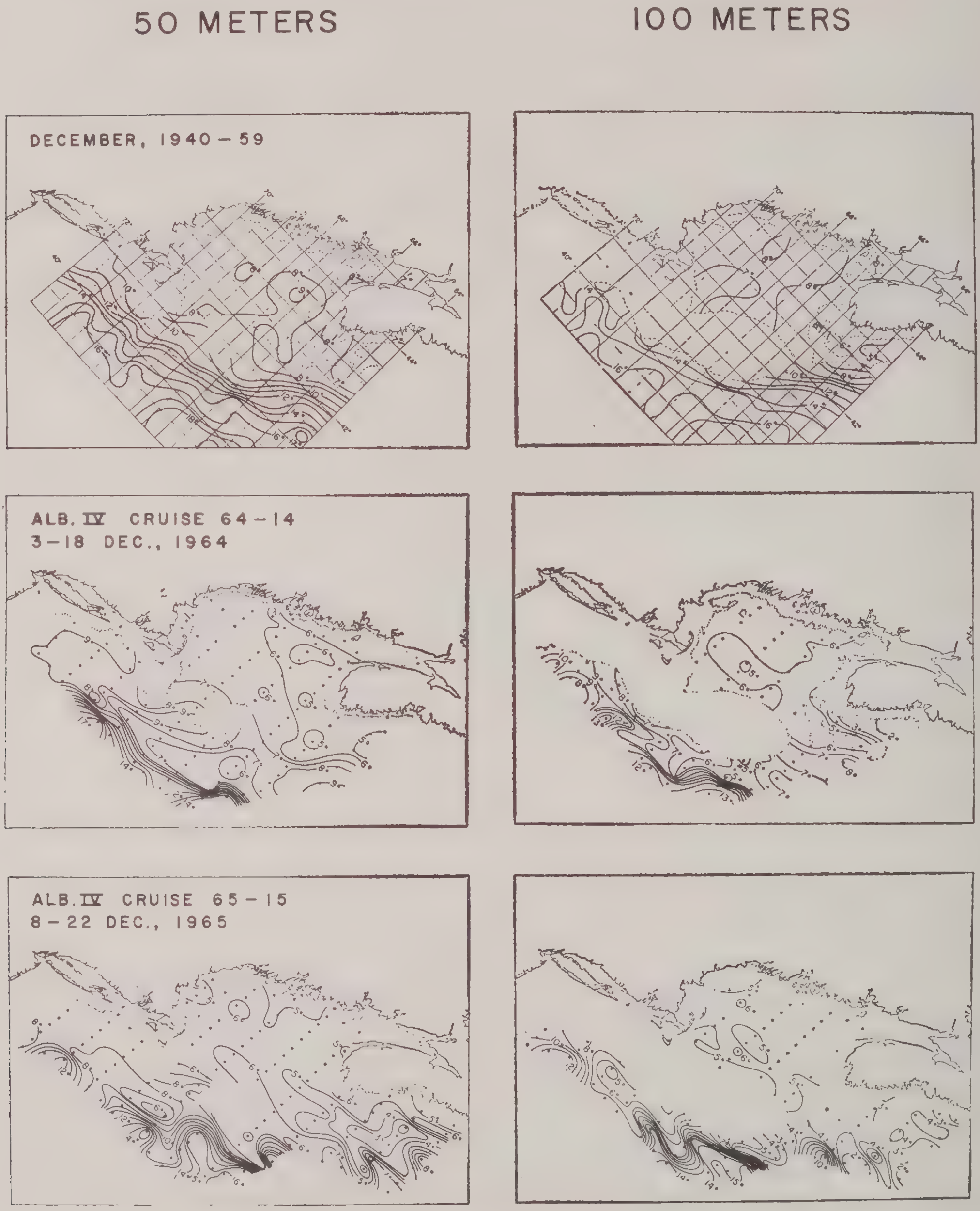

50 METERS
100 METERS
DECEMBER, 1940 — 59
ALB. IV CRUISE 64 — 14
3 — 18 DEC., 1964
ALB. IV CRUISE 65 — 15
8 — 22 DEC., 1965

Fig. 10. Temperature distribution at 50 and 100 m, December 1940–59, 1964, and 1965.

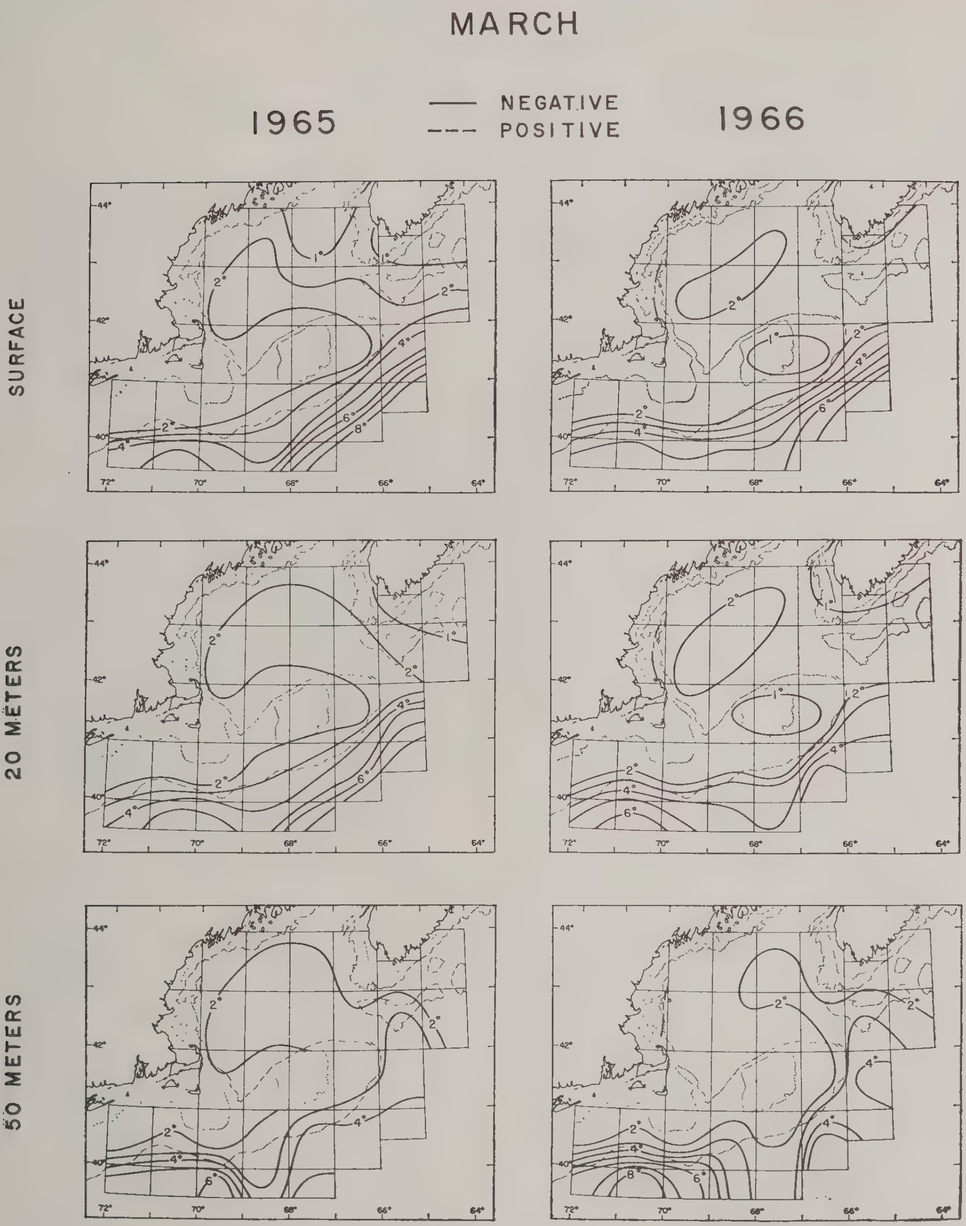

MARCH
1965
NEGATIVE
POSITIVE
1966
SURFACE
20 METERS
50 METERS
44°
42°
40°
72°
70°
68°
66°
64°
1°
2°
4°
6°
8°

Fig. 11. Temperature anomalies at the surface, 20 m, and 50 m, March 1965 and 1966.

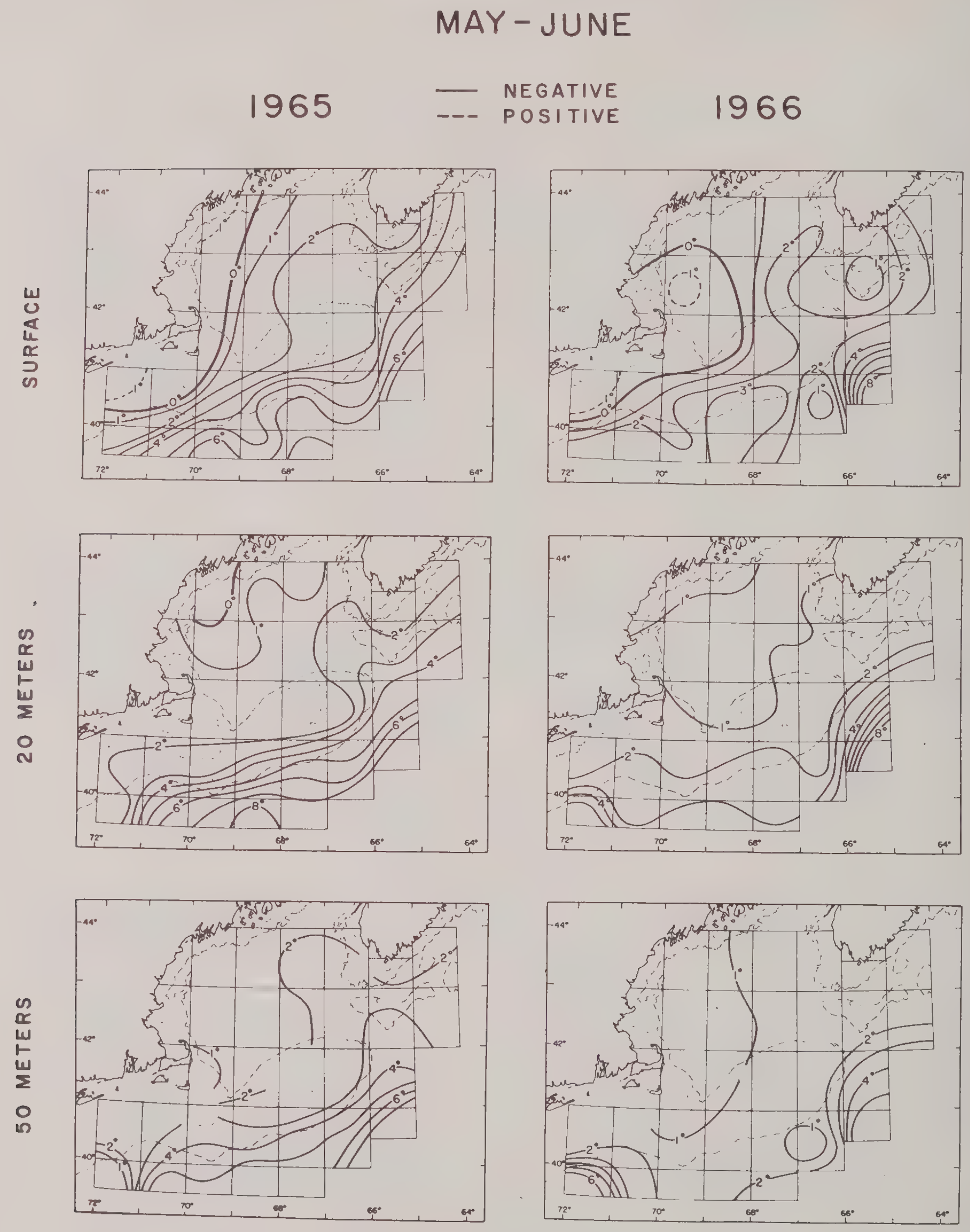

MAY - JUNE
1965
— NEGATIVE
--- POSITIVE
1966
SURFACE
20 METERS
50 METERS
44°
42°
40°
72°
70°
68°
66°
64°

Fig. 12. Temperature anomalies at the surface, 20 m, and 50 m, May -June 1965 and 1966.

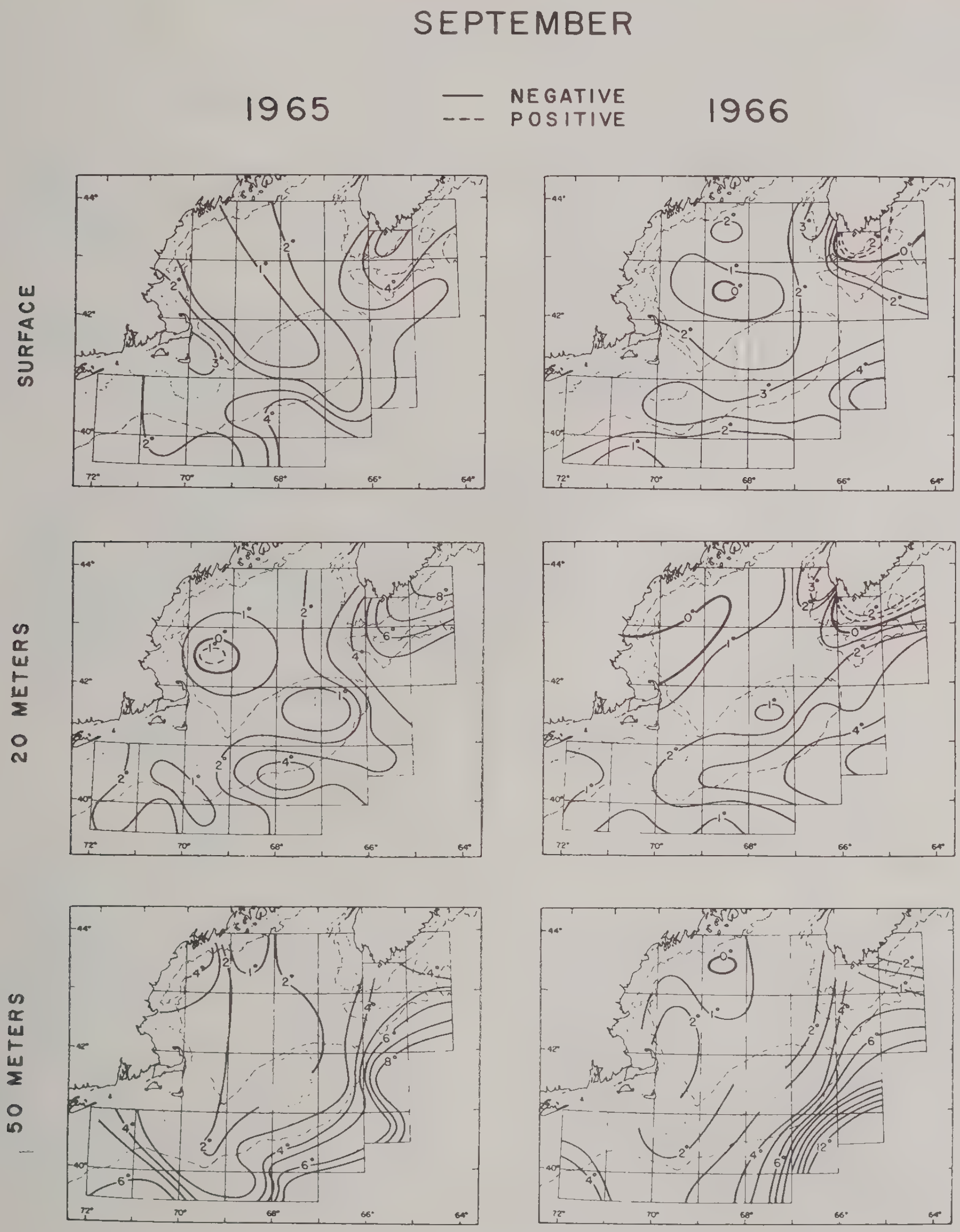

SEPTEMBER
1965
— NEGATIVE
--- POSITIVE
1966
SURFACE
20 METERS
50 METERS
44°
42°
40°
72°
70°
68°
66°
64°

Fig. 13. Temperature anomalies at the surface, 20 m, and 50 m, September 1965 and 1966.

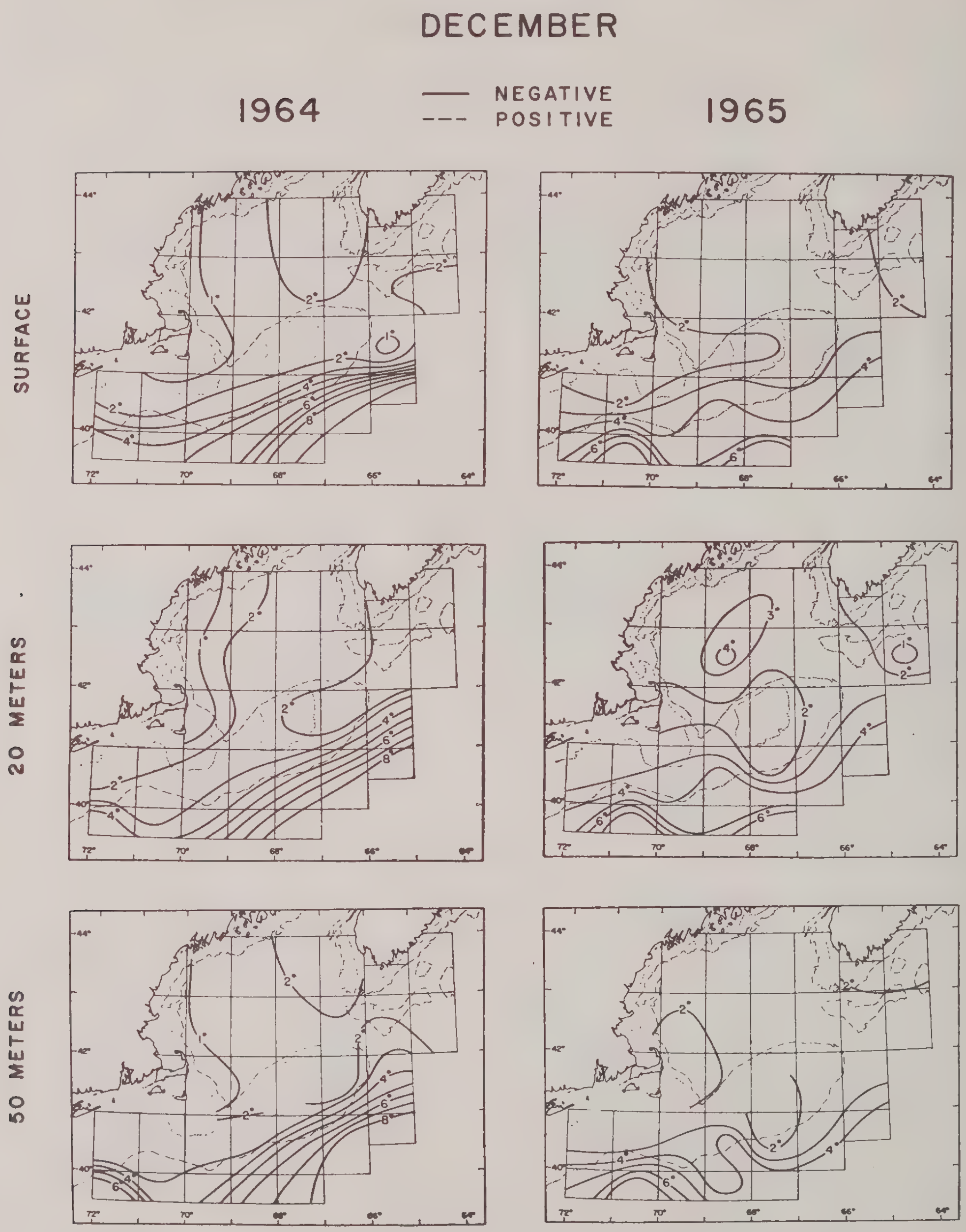

DECEMBER
1964
NEGATIVE
POSITIVE
1965
SURFACE
20 METERS
50 METERS
44°
42°
40°
72°
70°
68°
66°
64°
1°
2°
3°
4°
6°
8°

Fig. 14. Temperature anomalies at the surface, 20 m, and 50 m, December 1964 and 1965.

In general, the greatest negative anomalies occurred south of Georges and Browns Banks. The boundary between high and low negative values roughly paralleled the 100-m isobath. The most marked exception to this situation was the occurrence of an area of relatively high negative anomalies at the 20-m level southwest of Nova Scotia in September 1965. The highest positive anomalies (>2°C) occurred in this same general area at the surface and 20-m in September 1966.

A surface-water cooling trend commencing in the middle 1950's has been observed at Atlantic coast stations from Halifax, Nova Scotia to Cape Hatteras (Lauzier 1965; Stearns 1965). This cooling trend has been most pronounced along the coast between Cape Sable and Long Island. One of the longest series of inshore temperature records are the observations made at Boothbay Harbor, Maine. These daily records, maintained since 1905, show that preceding the current cooling period, a significant warming period began about 1945 and reached a maximum during 1952–53. This warming trend was discernible in offshore data as well (Taylor, Bigelow, and Graham 1957).

In Fig. 15 are plotted temperature anomalies at the surface, 20-m, and 50-m during March 1953 (*Albatross III* Cruise 46, 19 March–2 April) relative to the March 1940–59 mean. The anomalies in all areas and at all depths were positive, but tended to be highest over shoal water areas.

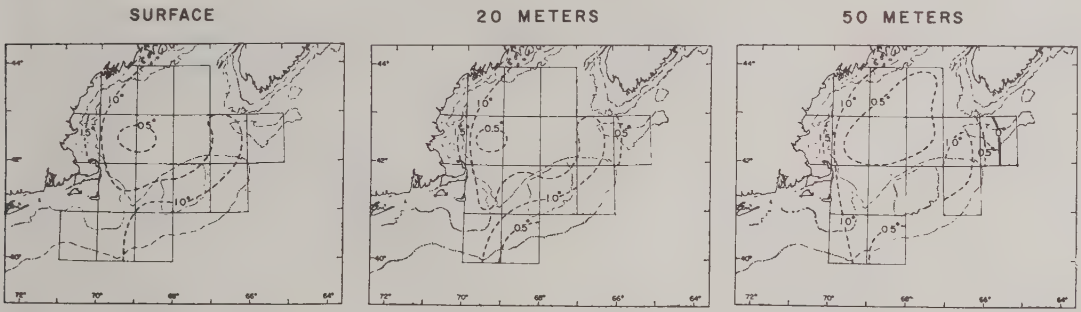


Fig. 15. Temperature anomalies at the surface, 20 m, and 50 m, March 1953.

Seasonal surface-temperature curves based on monthly mean temperatures at Boothbay Harbor, Maine, for the period 1940–59, 1953, 1964–66 are shown in Fig. 16. Temperature data for the period 1940–55 are from Bumpus (1957). Subsequent data were obtained from the files at the Woods Hole Oceanographic Institution. With the exception of January and February 1964 and May 1965, all monthly mean temperatures in the 1960's were lower than the 1940–59 means. The seasonal magnitude of the negative anomalies at Boothbay Harbor and of the anomalies observed in the immediate offshore region during the 1960 survey cruises were similar. For example, the May–June survey data showed a slight positive anomaly for the quadrangle immediately adjacent to Boothbay Harbor in 1965 and May was the only month in 1965 in which the Boothbay monthly mean temperature was not lower than the 1940–59 mean. During most months in the 1960's the negative anomalies in deep-water offshore areas were greater than the negative anomalies at Boothbay Harbor.

The 1953 monthly mean temperatures at Boothbay Harbor were appreciably higher than the 1940–59 means. In March 1953 the positive anomaly at Boothbay Harbor was greater than that in any offshore area. A comparison of monthly mean temperatures at Boothbay Harbor from 1906 to 1927 and 1928 to 1949 by Taylor *et al* (1957) showed significant increases in winter temperatures (November–February) but slight decreases in summer temperatures (July–September) during the latter period. In 1953, although the anomalies were greater in the winter, the anomalies were positive for all months. The similarity of the temperature trends at Boothbay Harbor and offshore areas in the 1960's indicate that at least during the peak of the warming period temperatures were higher during all months in the majority of offshore areas as well.

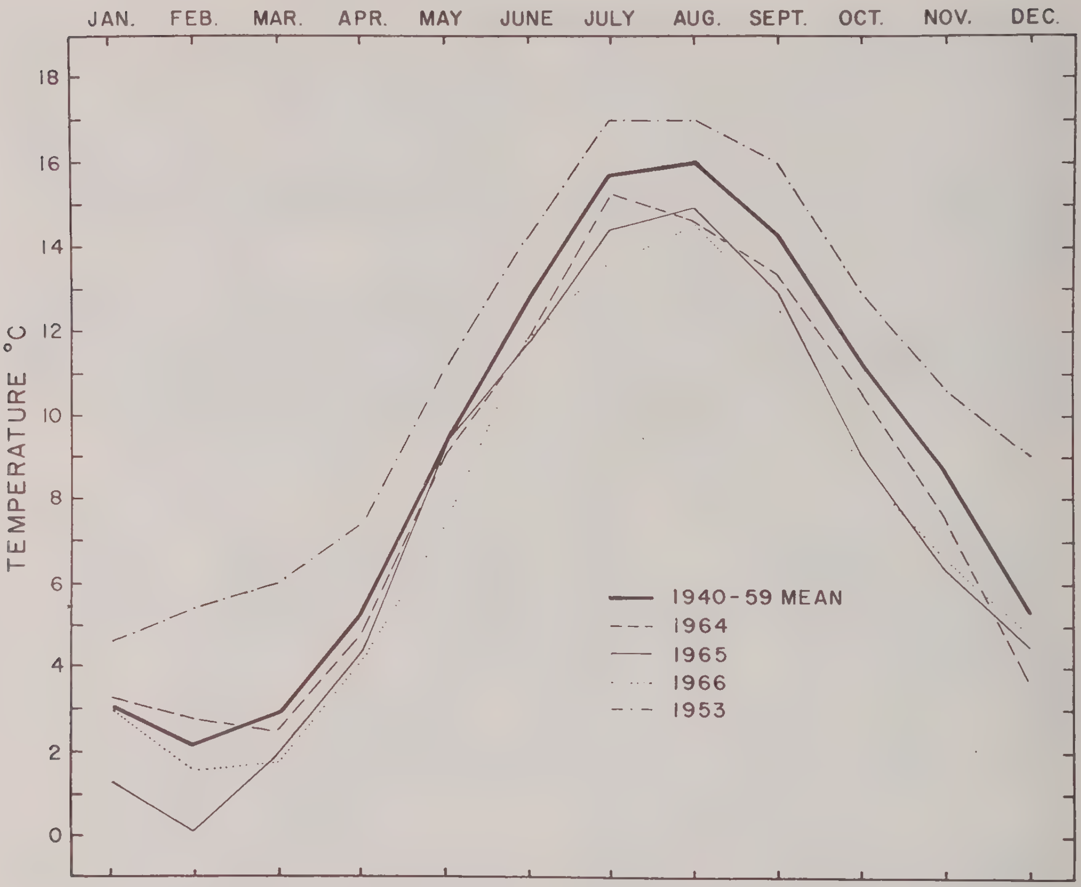


Fig. 16. Seasonal temperature curves, Boothbay Harbor, Maine, 1940–59, 1953, 1964, 1965, and 1966.

Discussion

Earlier publications give clear evidence of cyclic change in ocean temperatures off New England and the Maritime Provinces. A comparison of offshore temperatures for 1953–54 and 1912–26 made by Taylor *et al* (1957) indicated an increase of from 0.5° to 2.0°C throughout the water column since 1912–26 in most parts of the Gulf of Maine. Lauzier (1965) showed that trends in bottom temperature on the Scotian Shelf and in the Bay of Fundy were similar to the surface temperature trends at St. Andrews, New Brunswick and Boothbay Harbor, Maine, although the rate of cooling during the late 1950's and early 1960's was more pronounced within the bottom water.

The data from the 1964–66 survey cruise further document the fact that similar temperature fluctuations occurred offshore and within water masses as well as at the surface. Although temperature anomalies tended to be greater in the deeper water along the edge of the Continental Shelf, the trends in inshore temperature resembled those in most offshore areas. Clearly we may now place more reliance on the use of inshore temperature observations as an index to offshore conditions.

Taylor *et al* (1957) concluded that the composition of the fish and invertebrate fauna in the Gulf of Maine had undergone no obvious general change as a consequence of the warming trend during the early 1950's. To my knowledge, there is also no evidence of a conspicuous change in faunal composition during the current cooling period. These temperature fluctuations do, nevertheless have significant effects.

For example, the timing of haddock spawning appears to be regulated in part by temperature. Fish egg and larval surveys conducted during 1953, 1955, and 1956 showed that the main spawning on Georges Bank was in March and April at prevailing water temperatures of 4° to 7°C (Colton and Temple, 1961). Spawning began at about the time of the start of vernal warming. In Table I are tabulated the March and April mean temperatures at Boothbay Harbor during 1953, 1955, and 1956 and the March/April ratio of egg abundance on Georges Bank during these same years. As March and April mean temperatures decreased during succeeding years the time of maximum spawning on Georges Bank was delayed correspondingly as indicated by the decrease in the March/April egg abundance ratio.

TABLE 1. March and April mean temperatures at Boothbay Harbor and the March/April ratio of haddock egg abundance on Georges Bank, 1953, 1955, and 1956.

Year	Temperature, °C March	Temperature, °C April	March/April egg abundance ratio
1953	6.1	7.5	7.3
1955	4.2	6.9	2.7
1956	3.2	5.3	1.3

An unpublished analysis of the distribution and abundance of *Calanus finmarchicus* based on collections made during the 1953 and 1955 egg and larval surveys revealed a difference also in the timing of the vernal augmentation of the stock of *Calanus* during these 2 years. The developmental stages collected in the cruises of 1953 indicate that the main spawning of the overwintering stock occurred in February and that the progeny of that spawning reached maturity in late May. In 1955 the overwintering stock did not spawn until March and the second generation did not reach maturity until late June. It is highly probable that spawning time and availability of food organisms of suitable size influence the survival rate of larval and juvenile fish.

Lauzier (1965) suggested that variations in the degree of upwelling due to fluctuations in the intensity of westerly winds could effect short-term changes in annual temperatures along the Canadian Atlantic coast. The nature of the distribution of temperature and negative anomalies observed during the survey cruises of 1964–66 however, give evidence that temperature trends recorded at most Atlantic coast stations are not caused by variations in local conditions such as upwelling and river runoff, but are due in large measure to changes in the relative position and degree of mixing of coastal and oceanic water masses. An example is the fact that the gradient of negative anomalies which occurred off the edge of the Continental Shelf was least during September, a period in which indications of intrusions of Slope and Gulf Stream water onto the southern edge of Georges Bank have been most frequent (Colton, 1961). It would appear also that the change in sign of the anomalies off the southwest coast of Nova Scotia in September 1965 (negative) and 1966 (positive) resulted from a variation in the degree of influx of Nova Scotian current water into this area during these years.

It has been postulated by Iselin (1940) and Stommel (1958) that the degree of mixing of coastal and oceanic water and the resulting warming or cooling of North Atlantic coastal water are related to fluctuations in the strength of the North Atlantic gyre. Bjerknes (1963) and Rodewald (1963) have related these changes in oceanic circulation to variations in atmospheric circulation due to changes in the relative strengths of the Bermuda-Azores High and the Icelandic Low. The cooling trends have been linked to a constriction and warming trends to an expansion of the warm oceanic water mass.

Summary

Although long-term mean temperatures were used to interpret conditions in a region characterized by short-term temperature fluctuations, the method appears to provide a measure of major temperature conditions to which specific cruise data may be compared.

The 20-year mean and specific-year seasonal and areal temperature trends were similar; minimum temperatures occurred in March and inshore and maximum temperatures in September and offshore.

During all seasons and at most locations and depths the 1964–66 temperatures were appreciably lower than the 1940–59 mean values. The magnitude of the negative anomalies was greatest in areas off the edge of the Continental Shelf. Temperatures in March 1953 were higher than the 1940–59 mean values.

The trends in offshore temperatures at the surface and within water masses paralleled trends in surface temperatures at Boothbay Harbor, Maine. These correlations justify the use of inshore temperature observations for indexing offshore conditions.

A delay in the timing of maximum haddock spawning on Georges Bank in 1955 and 1956 as compared with 1953, and of the vernal augmentation of the stock of *Calanus finmarchicus* in the Gulf of Maine during 1955 as compared with 1953 was attributed to decreasing temperatures.

The nature of the distribution of temperature and of negative anomalies observed in 1964–66 suggest that temperature trends recorded at most Atlantic coast stations depend in large measure on the relative position and degree of mixing of coastal and oceanic water masses.

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Recent Trends in Subsurface Temperatures in the Gulf of Maine and Contiguous Waters[1]

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ABSTRACT

A comparison was made of 1955–60 and 1961–66 monthly mean 200-m temperatures in eight 1-degree quadrangle areas in the Gulf of Maine and along the Continental Slope between Nova Scotia and Long Island. Temperatures were appreciably lower in all areas during the latter period. The subsurface temperature trends paralleled trends in surface temperatures previously documented. The distribution of temperature at 200 m along the edge of the Continental Shelf during March, May–June, and September 1965 and 1966 and the distribution of temperature, salinity, and dissolved oxygen on sections made across the Continental Shelf in September 1954, 1965, and 1966 showed that the cooling and warming trends are accompanied by changes in the composition of the subsurface water. Cold years occur when Slope Water is displaced or modified by Coastal Water of Labrador origin. Warm years occur when Slope Water borders upon the 200-m isobath and the ratio of Coastal to Central Atlantic Water is low.

INTRODUCTION

CLEAR EVIDENCE EXISTS of an alternation in sea surface temperatures along the coast of New England and the Maritime Provinces (Taylor et al., 1957; Lauzier, 1965; Stearns, 1965). A warming trend began in the early 1940's and reached a maximum during 1952–53. This rise in temperature has been followed by a cooling trend which has continued with only minor interruptions through 1967. Although less well-documented, similar warming and cooling trends have occurred offshore and within water masses (Taylor et al., 1957; Lauzier, 1965, 1967; Colton, 1968). Most of the published offshore observations have been confined to the Continental Shelf and to depths of 100 m or less. In this paper an analysis is made of the available subsurface temperature data in the Gulf of Maine and along the edge of the Continental Shelf from Nova Scotia to Long Island to determine if the trends observed in the surface layers are reflected in the deeper strata.

The subsurface layer, the upper depth limit of which is usually between 150 and 200 m, is relatively isolated from seasonal factors such as wind stirring and solar heating. Unlike the surface layer, which is characterized by pronounced seasonal variations and a complex and unstable temperature and salinity structure, the structure of the subsurface layer is relatively stable and governed by the waters adjacent to it.

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Our interest in subsurface temperature trends stems from the fact that if these trends parallel those in the surface layers, the faunal communities in the deeper waters of the Gulf of Maine and the Continental Slope are subject to long-term temperature variations similar to those experienced by the fauna in relatively shoal areas of the Continental Shelf. Furthermore, since the temperature–salinity characteristics of subsurface water masses can be used to define their component water types, it should be possible to determine the sources of the subsurface water during periods of warming and cooling and thus the direct cause of the temperature change.

THE DATA

A tabulation of temperature data from the file of bathythermograph and oceanographic station observations at the Woods Hole Oceanographic Institution revealed that during the warming period of 1945–53 the number of observations was insufficient to determine valid average subsurface temperatures for any location within the area of concern. Since 1955 the data appear to be adequate to determine monthly subsurface temperatures if several year's observations within 1-degree quadrangles are averaged. Monthly mean 200-m temperatures were determined for the periods 1955–60 and 1961–66 within the eight 1-degree quadrangle areas shown in Fig. 1. Areas I–III are over the three deep basins of the Gulf of Maine, area IV is at the mouth of the Northeast Channel which separates Georges and Browns banks, and areas V–VIII are along the Continental slope. Observations were relatively few for any month within a given year in any quadrangle and these observations were generally weighted in favor of certain days (dates). To offset possible

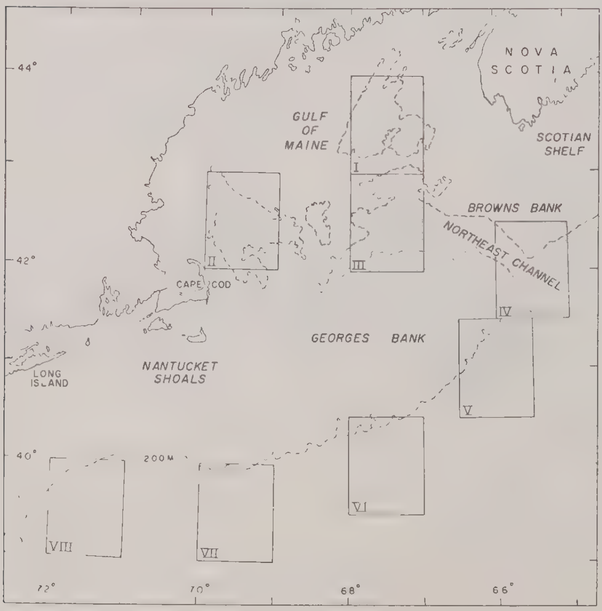

FIG. 1. The location of the eight 1-degree quadrangle areas.

bias in determining monthly means, all data for a given day were averaged and the 6-year monthly means based on the daily means rather than on the total number of observations.

The 6-year monthly mean temperatures at 200 m in the eight areas are plotted in Fig. 2 and 3. The months and years in which temperature data were obtained are indicated by check marks. The long-term annual mean 200-m temperatures are shown by a broken line. These long-term values are from Schroeder (1963) and are based on 1-degree quadrangle averages of all available temperatures in the Woods Hole Oceanographic Institution data collection until the end of 1962. For areas IV, V, and VI which do not coincide with the whole-degree latitude–longitude quadrangles used by Schroeder, long-term 200-m temperature values from overlapping whole-degree quadrangles were averaged.

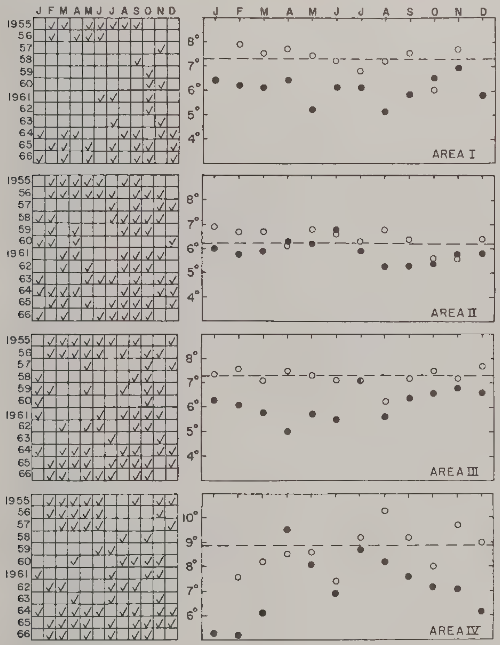

Fig. 2. Monthly and annual mean temperatures at 200 m, areas I–IV. The 1955–60 monthly means are shown by open circles, the 1961–66 monthly means by solid circles. The long-term annual means are indicated by a broken line. Check marks indicate the months and years in which observations were made.

With only a few exceptions (April: areas II and IV; June: area II; July: area III; September: area V; October: areas I and V; and November: area II) the 1960–66 monthly mean 200-m temperatures were lower than the corresponding monthly mean temperatures for 1955–60. Six of these eight anomalies were in months which included 1963 observations. In this year there was a temporary interruption in the downward trend of sea surface temperatures both inshore at Boothbay Harbor, Maine (Welch, 1967), and offshore over the Grand Banks and Georges Bank (Lee et al., 1967). In addition the data of Schopf (1967, Fig. 2) show that bottom temperatures on the Scotian Shelf, Georges Bank, Nantucket Shoals, and in the Gulf of Maine were appreciably warmer in July, August, and December 1963 than in these months during 1964 and 1965.

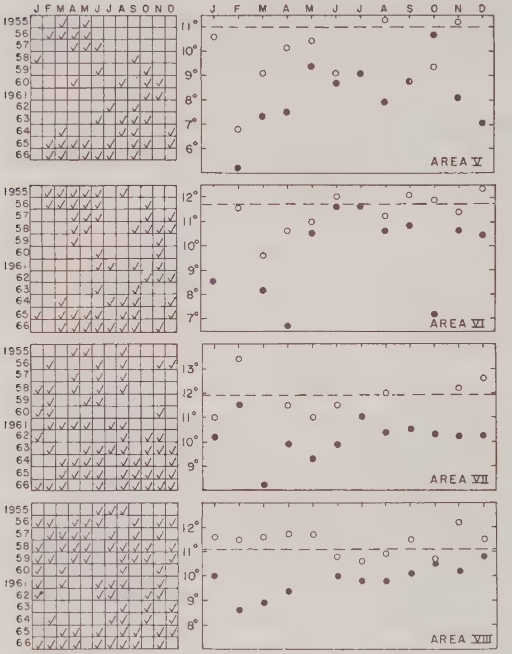

FIG. 3. Monthly and annual mean temperatures at 200 m, areas V–VIII. The 1955–60 monthly means are shown by open circles, the 1961–66 monthly means by solid circles. The long-term annual means are indicated by a broken line. Check marks indicate the months and years in which observations were made.

No consistent seasonal trend existed in the 200-m monthly mean temperatures or in the magnitude of the monthly mean temperature differences for the two time periods in any of the areas. The monthly temperature variation and the magnitude of the monthly temperature differences in the two time periods were least in area II and tended to be greater along the Continental Slope than within the Gulf of Maine. With the exception of area V, yearly mean temperatures based on 1955–60 data closely paralleled Schroeder's long-term means. In area V, the 1955–60 yearly mean was appreciably lower (2.3 degrees C) than the long-term mean. With the exception of area II, the 1960–66 yearly mean temperatures were well below Schroeder's long-term means. In area II, the 1961–66 yearly mean was only slightly lower (0.3 degrees C) than the long-term mean.

Seasonal surface-temperature curves based on monthly mean temperatures at Boothbay Harbor, Maine, for 1955–60 and 1961–66 (Fig. 4) show temperature trends similar to those in the subsurface waters. In most months and areas, however, the difference in the mean 200-m temperatures for the two 6-year periods was greater than the difference in mean surface temperatures at Boothbay Harbor. Only in area II was the yearly mean difference between the two time periods less at 200 m (0.6 degrees C) than at Boothbay Harbor (0.9 degrees C).

In Fig. 5 the distribution of temperature at 200 m along the edge of the Continental Shelf and in the Northeast Channel during March, May–June, and September 1965 and 1966 is compared with the long-term annual mean and minimum 200-m values in this area. The 1965 and 1966 temperature

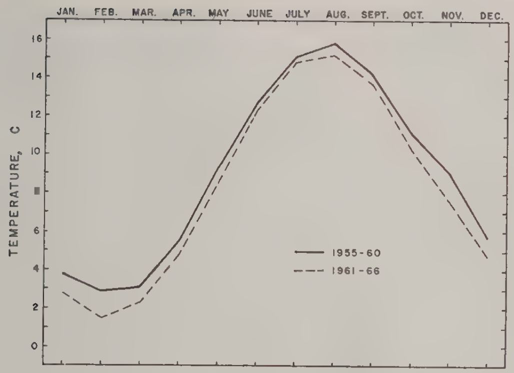

FIG. 4. 1955–60 and 1961–66 mean seasonal temperatures, Boothbay Harbor, Maine.

distributions are based on in situ bathythermograph observations obtained during quarterly environmental surveys conducted by the U.S. Bureau of Commercial Fisheries (Colton et al., 1968). The long-term distributions are based on the average and the minimum temperatures for 1-degree quadrangles given by Schroeder (1963). In both 1965 and 1966 the monthly temperatures adjacent to the 200-m isobath were lower than the long-term mean. In most cases the 1965 and 1966 monthly temperatures were higher than the long-term minimum temperatures. In March 1966, however, the 200-m temperatures were lower than the long-term minimum temperatures in sections adjacent to the 200-m isobath off southern New England, the southeast part of Georges Bank, and the Scotian Shelf.

If we consider the contour of the 9 C isotherm at 200 m to be the northern limit of Slope Water (Worthington, 1964), the long-term annual mean temperature distribution at 200 m would indicate that, in general, Slope Water borders upon the 200-m isobath from Cape Hatteras east to approximately 64°00′W. The distribution of temperature at 200 m during 1965 and 1966 indicates that in these years the northern boundary of the Slope Water was considerably south of its average position. Worthington (1964) concluded that any water colder than 9 C at 200 m could be traced to the Labrador Basin. It would appear that the southerly shift in the normal position of the Slope Water in 1965 and 1966 was due to an abnormal influx of Coastal Water of Labrador origin.

The available salinity data are not sufficient to establish subsurface salinity norms for the area as a whole or to compare the 1955–60 and 1961–66 mean salinity characteristics of the subsurface water in any of the eight 1-degree quadrangle areas on either a monthly or yearly basis. A few oceanographic section data are suitable, however, for a comparison of the inshore and offshore distribution of chemical and physical properties at the end of the warming trend and during the current cooling trend. In Fig. 6 the distribution of temperature, salinity, and dissolved oxygen on sections made along meridian 65°30′W by the *Albatross IV* in September 1965 and 1966 is compared with the distribution of these properties on a section made along meridian 65°00′W by the *Atlantis* in September 1954.

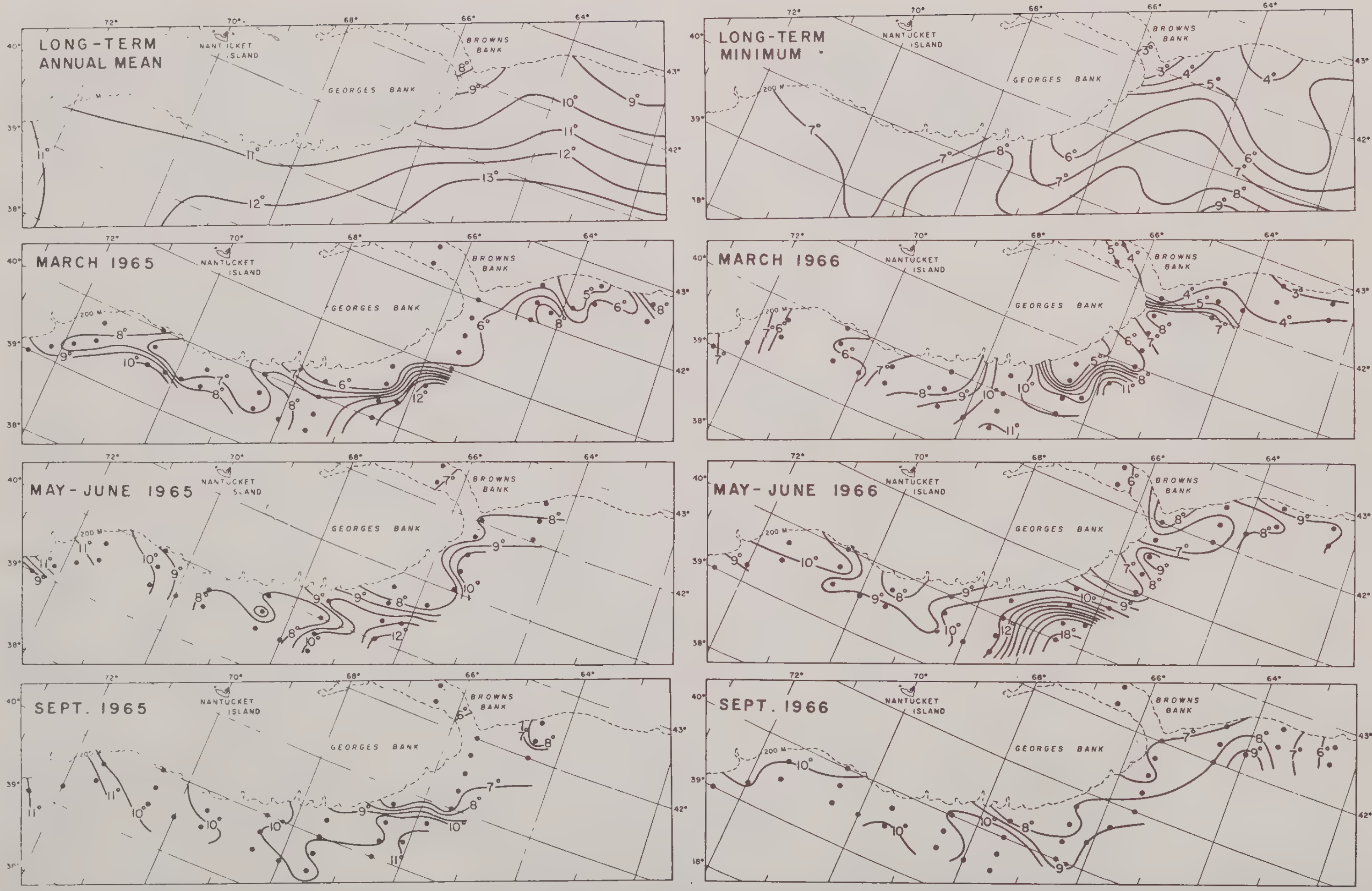
LONG-TERM ANNUAL MEAN
LONG-TERM MINIMUM
MARCH 1965
MARCH 1966
MAY-JUNE 1965
MAY-JUNE 1966
SEPT. 1965
SEPT. 1966
NANTUCKET ISLAND
GEORGES BANK
BROWNS BANK
200 M
72°
70°
68°
66°
64°
40°
39°
38°
43°
42°

FIG. 5. Comparison of the temperature distribution at 200 m during March, May–June, and September 1965 and 1966 with long-term annual mean and minimum distributions.

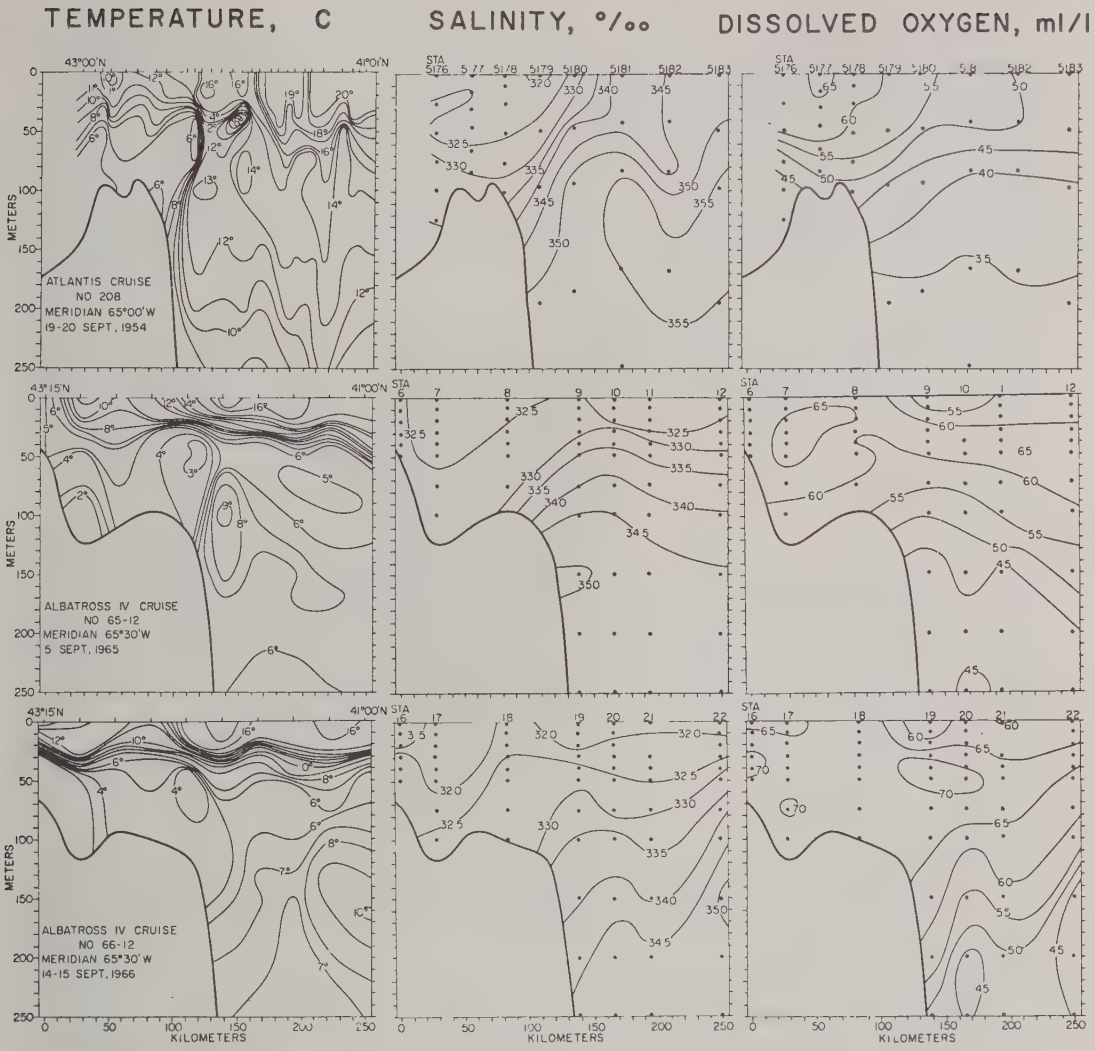

FIG. 6. Temperature, salinity, and dissolved oxygen profiles, September 1954, 1965, and 1966.

Subsurface temperatures and salinities were appreciably higher in 1954 than in 1965 and 1966. At the southern-most stations, the 1954 temperature and salinity values were higher in the surface layer as well. If we consider a temperature of 9 C and a salinity of 35‰ at 200 m as roughly defining the northern limit of Slope Water, the Slope Water boundary coincided with the 200-m isobath in 1954, but was south of 41°00′N lat in 1965 and 1966. Dissolved oxygen values at corresponding depths were appreciably higher in 1965 and 1966 than in 1954. The dissolved oxygen concentrations at depths of 100, 150, and 200 m south of the Continental Shelf corresponded closely to those typical of Slope Water in 1954 and to those typical of Coastal Water in 1965 and 1966 (McLellan, 1957, Table II).

Temperature–salinity data at 150, 200, and 250 m for the five most southerly *Atlantis* stations in September 1954 and for the four most southerly *Albatross IV* stations in September 1965 and 1966 are plotted in Fig. 7. The *Albatross IV* data are based on observed values at these depths whereas the *Atlantis* data are based on interpolated values. The temperature–salinity curves for Central Atlantic Water, Slope Water, and Coastal Water are also shown. The approximate depths in meters at which waters of various temperature–salinity characteristics are found are indicated by numbers adjacent to the curves. The Central Atlantic Water curve is from Iselin (1936) and is based on observations made in the western Sargasso Sea. The Slope Water curve of Iselin (1936) is for waters off Chesapeake Bay. The Slope Water curve of McLellan (1957) is for waters off the Scotian Shelf. The Coastal Water curve (McLellan, 1957) is based on observations made in the Cabot Strait. In describing this water Worthington (1964) used the term "Labrador-Coastal" instead of "Coastal" to indicate that this water is formed by a mixture of Labrador and Slope Water in the region immediately west of the Grand Banks and to distinguish this subsurface water from the surface water over the Continental Shelf. An excellent summary of the temperature–salinity characteristics, composition, and origin of these water masses is given by McLellan (1957).

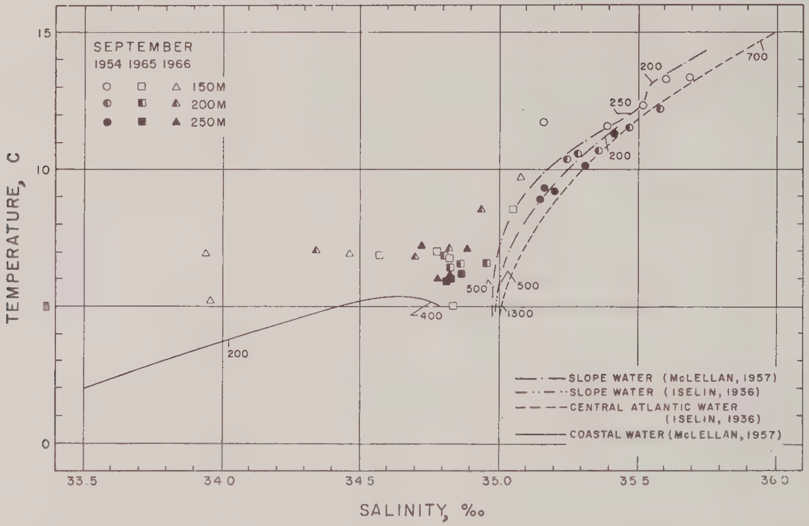

FIG. 7. Temperature–salinity relations at *Atlantis* stations 5179–5183, September 1954 and *Albatross IV* stations 9–12 and 19–22, September 1965 and 1966.

The temperature–salinity relations confirm the conclusions drawn from the section data. The subsurface water bordering the Continental Shelf south of Browns Bank in September 1954 was Slope Water and that in September

1965 and 1966 was Coastal Water. The temperature–salinity characteristics of the Slope Water in 1954 coincide more closely with the Slope Water curve of Iselin (1936) than with that of McLellan (1957) and show a greater constituent ratio of Central Atlantic Water than in areas to the east. Indeed, a few of the *Atlantis* station plots fall to the right of the Central Atlantic curve, but these points possibly represent errors in interpolation of salinity between the widely spaced sample depths. The majority of the 1965 and 1966 temperature–salinity values lay between those of the characteristic Coastal Water curve near its area of formation and those of the Coastal Water curve near its western limit of occurrence (Grampus station 10352, McLellan, 1957, fig. 6). The few values which fell in the proximity of the Slope Water curve were based on data from the isolated pools of relatively high temperature and salinity water at *Albatross IV* stations 9 and 22.

DISCUSSION

The cooling and warming of subsurface waters along the Continental Slope between Nova Scotia and Long Island are due to changes in the composition of these waters. Cold years occur when Slope Water is displaced or modified by Coastal Water of Labrador origin. Warm years occur when the Slope Water borders on the 200-m isobath and its constituent ratio of Coastal to Central Atlantic Waters is low. Bigelow (1927) pointed out that the relatively high temperature and salinity of the bottom water in the deep basins of the Gulf of Maine indicated its offshore origin. He concluded that this water, which enters the Gulf of Maine intermittently via the Northeast Channel, has its source along the slope of the Scotian Shelf and that the temperature and salinity variations of the deep water in the Gulf of Maine are due to fluctuations in the volume of, rather than in the temperature and salinity of, this inflowing drift. The more recent data presented in this paper demonstrate that the temperature–salinity characteristics of the subsurface waters adjacent to the mouth of the Northeast Channel vary; they are colder and less saline during periods of cooling than during periods of warming. Thus, it would appear that trends in subsurface temperatures within the Gulf of Maine can be traced to variations in the composition of these offshore waters as well as to the volume of their indraft through the Northeast Channel. This view is substantiated by the observations of L. M. Lauzier (unpublished) showing that in the deep waters in the Bay of Fundy and Emerald Basin, warming periods were accompanied by an increase in salinity and cooling periods were accompanied by a decrease.

Further evidence that the subsurface temperature trends observed within the Gulf of Maine are linked to variations in the composition of the subsurface waters bordering the Continental Shelf is afforded by the fact that the magnitude of the differences between 1955–60 and 1961–66 monthly mean temperatures was least in Area II. This area, which includes Murry and Wilkinson basins, is the most distant from the Northeast Channel. In addition, the relatively shoal sill to the east of these basins further restricts horizontal communication with the open sea.

These subsurface data support the conclusion drawn from an analysis of temperature trends in the surface layers in the same area (Colton, 1968); that is, these temperature trends depend in large measure on the relative position and the degree of mixing of coastal and oceanic water masses. There is evidence to the effect that the changes observed in the relative position and degree of mixing of Coastal, Slope, and Central Atlantic waters along the Continental Slope are due to variations in atmospheric conditions that result from changes in the position and relative strength of the Icelandic Low. Lee et al. (1967) have postulated that surface temperature anomalies and their fluctuations over the Grand Banks and Georges Bank can be explained by advection caused by surface winds. Worthington (1964) has suggested that variations in barometric pressure as well as surface winds could cause advective movements of subsurface waters off the Scotian Shelf. It may be, however, that these advective movements of surface and subsurface water masses and the subsequent warming and cooling trends are more directly related to fluctuations in the strength of the North Atlantic Gyre, as suggested by Iselin (1940) and Stommel (1958). In this connection, an analysis of long-term trends in the volume transport of the Florida Current would be most useful.

Existing hydrographic and meteorological data are too fragmentary for a detailed study of long-term fluctuations in the distribution and degree of mixing of coastal and oceanic water masses in the area between Nova Scotia and Long Island. It is doubtful that adequate data for such an analysis will be available in the forseeable future. With existing instrumentation it should be possible, however, to monitor subsurface hydrographic conditions in a critical area such as the Northeast Channel. Such data, even if they consisted solely of time-series bottom temperatures, would greatly increase our capability to measure and predict trends in both subsurface and surface temperatures in the Gulf of Maine and contiguous waters.

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I thank Miss E. H. Schroeder for access to the temperature data collection at the Woods Hole Oceanographic Institution; Mr W. R. Welch for use of the Boothbay Harbor temperature data; and Mr L. Worthington and Dr L. M. Lauzier for critical reading of the manuscript.

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EPIZOOTIOLOGY OF *MINCHINIA COSTALIS* AND *MINCHINIA NELSONI* IN OYSTERS INTRODUCED INTO CHINCOTEAGUE BAY, VIRGINIA

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ABSTRACT

The introduction of Crassostrea virginica *into Chincoteague Bay, at Franklin City, Virginia, was studied in relation to haplosporidan epizootics from September, 1963 to September, 1966. The introduced oysters (1962 year class) were from Harris Creek, eastern shore of Chesapeake Bay, an area where* Minchinia nelsoni *and* M. costalis *(Haplosporida: Haplosporidiidae) have not been found. Eight introductions of about 1200 oysters each were made in September, December, March, and June during 2 successive years.*

Generally, mortality followed a similar course among oysters in all introductions. Oysters in the two quarterly introductions in September died during the following August-September, after 11-12 months of exposure, in numbers that indicated an epizootic. Other quarterly pairs of introductions in December, March, and June of both years also experienced similarly significant mortalities in the same August-September period, after 3-9 months exposure. Mortality was not significant during the winters following any of the introductions. The second mortality peak for all introductions came in May-June of the second summer of exposure. A relatively lower death rate persisted after the May-June epizootic until the end of the study. Total periods of exposure to Chincoteague Bay waters ranged from 16 months to 24 months and cumulative mortalities, to September 1966, ranged from 65.5 per cent to 76.5 per cent.

Among oysters introduced during the first year of the study, Minchinia nelsoni *was first observed in April of the first spring; its prevalence declined during May and June, then increased in July, August, and September preceding and concurrent with the first mortality peak. Among oysters introduced during the second year of the study,* M. nelsoni *was first seen in late July. Prevalence of the parasite increased during August and September, concurrent with the first mortality peak experienced by these oysters. The prevalence of* M. nelsoni *during the first and second winter of exposure was high in oysters examined, but accompanied by significant mortality. Prevalence of* M. nelsoni *in early May of the second spring dropped slightly but overlapped the first incidence of* M. costalis.

Prevalence of M. costalis *reached its peak (concurrent with heavy spore production) in May-June of the second year of exposure, during the second mortality peak, when* M. nelsoni *was also common. Concurrent plasmodial and spore infections of the two species were found during May and June. After early July,* M. costalis *was not found in oysters from any of the introductions. After the June mortality of the second year prevalence of* M. nelsoni *was low until the end of the study.*

The epizootiology of these parasites in Chincoteague Bay is compared with long-term studies by others in lower Chesapeake Bay, and Delaware Bay.

INTRODUCTION

After the discovery of the oyster haplosporidan termed "MSX" and later named *Minchinia nelsoni* (Haskin, Stauber, and Mackin, 1966), another haplosporidan, *Minchinia costalis* (Wood and Andrews, 1962), was described from oysters of Seaside Virginia. Subsequently, Andrews, Wood, and Hoese (1962) reported the epizootiology of *M. costalis* and *M. nelsoni* for sea-side areas of Virginia, and Andrews (1966, 1967) further described the effects of *M. nelsoni* on oyster populations of lower Chesapeake Bay, Virginia. Haskin, Canzonier, and Myhre (1965) described briefly the epizootics caused by *M. nelsoni* in Delaware Bay.

General epizootiological findings by these investigators were:

1) Two haplosporidan parasites of oysters exist in coastal waters of the eastern United States.

2) These parasites are found in high prevalences in certain oyster populations and may cause severe oyster mortalities.

3) Mortality patterns associated with these parasites are usually repetitious yearly and, to some degree, predictable.

4) A possible way to re-establish oyster populations in epizootic areas is to seek innate resistance in some percentage of the survivors and develop a resistant stock from the progeny of these survivors (Haskin, personal communication, 1967). Andrews (1966) expressed this concept as "raising herd immunity on a genetic basis."

Considerable work has been done on the history (Haskin, 1962; Haskin *et al.*, 1965; Mackin, 1961; Andrews, 1967), morphology (Haskin *et al.*, 1966; Couch, Farley, and Rosenfield, 1966; Couch, 1967), portions of the life cycle (Myhre, 1966; Myhre, personal communication, 1967; Farley, 1967), and histochemistry (Eble, 1966) of these parasites.

Previous studies (Wood and Andrews, 1962; Haskin *et al.*, 1966) suggested that Chincoteague Bay was an enzootic-epizootic area for *Minchinia nelsoni* and *M. costalis*. Our objectives were: 1) to determine annual and seasonal parasite prevalences in susceptible oysters; 2) to determine the relationships of season of introduction and length of exposure to detection of infections and mortalities; 3) to determine cumulative mortality in introduced populations after varying periods of exposure. This paper reports the results of this 3-year epizootiological study of *M. nelsoni* and *M. costalis* and compares the epizootiology in Chincoteague Bay with that in areas studied by others.

METHODS

Beginning in September, 1963, experimental groups of oysters were introduced at 8 quarterly intervals, over a period of 2 years, into Chincoteague Bay, Virginia, and held there for varying periods of time (Table 1). The first 4 introductions (September, 1963 — June, 1964) were duplicated chronologically by the last 4 (September, 1964 — June, 1965). A study year was from 1 September to 31 August. The oysters (1961 year set) were obtained from Harris Creek, a portion of Chesapeake Bay, where *Minchinia nelsoni* and *M. costalis* have not yet been found. A sample of 50 oysters from each introduction was examined microscopically before exposure in Chincoteague Bay. No haplosporidans were found in any of the 8 quarterly base samples, nor in any of the trayed control oysters kept in Harris Creek and examined periodically during the second year of introductions. Mortalities of these control oysters were extremely low.

Each introduction consisted of approximately 1200 oysters distributed among 4 wire trays—about 300 to 400 per tray. These trays were suspended about 1 foot above the bottom to reduce siltation and to prevent predation. Silt accumulations and fouling organisms were removed at each sampling period. One tray of each introduction was used throughout the study for mortality observations

TABLE 1. *Periods of exposure and cumulative mortalities of trayed Harris Creek oysters maintained in Chincoteague Bay.*

Introductions	Date introduced	Date terminated	Exposure time (months)	Cumulative mortality (%)
1	Sept. 1963	Sept. 1965	24	70.5
5	Sept. 1964	Sept. 1966	24	75.5
2	Dec. 1963	Sept. 1965	22	73.8
6	Dec. 1964	Sept. 1966	22	70.4
3	Mar. 1964	Sept. 1965	19	65.2
7	Mar. 1965	Sept. 1966	19	73.8
4	June 1964	Sept. 1965	16	76.5
8	June 1965	Sept. 1966	16	73.1

only, and was not sampled. Twice each month the observation trays were raised, and the dead oysters counted and removed. Total monthly (cumulative) mortalities of each introduction were determined. Dead oysters (gapers with remaining tissues) found in the observation trays were fixed, sectioned, and examined for haplosporidans.

The remaining 3 trays in each introduction contained about 900 oysters. Each month 25 oysters of each introduction were taken randomly from among the 3 trays. Oysters were fixed in Davidson's fixative, sectioned and stained with Harris' hematoxylin, eosin, and Ziehl's fuchsin (Farley, 1965). Single sections of 7 μ from the area of the gills, palps, and stomach of each oyster were examined for *M. costalis* and *M. nelsoni.* Percentage of infection of monthly samples ($n = 25$ oysters per introduction) is expressed either as initial incidence (first level of infections for each introduction) or prevalence (monthly levels of infection).

Oysters of monthly samples were diagnosed according to the method of Ray (1952) for the presence of the fungal pathogen, *Dermocystidium marinum* (Mackin, Owen, and Collier, 1950), a species whose generic designation has recently been changed to *Labyrinthomyxa* (Mackin and Ray, 1966). No fungal infections were found in samples of oysters from this study.

MORTALITY OF OYSTERS

The mortality patterns in introduced oyster populations are described first, followed by the incidences and prevalences of *Minchinia costalis* and *M. nelsoni* as probable causes of mortalities.

The quarterly introductions were numbered consecutively from 1 through 8. Curves of percentage monthly mortality for each introduction are presented in Figure 1.

Oysters introduced in September 1963 and 1964 did not die in significant numbers until the summer and early fall (curves 1, 5 — lowermost curves in Fig. 1). Oysters introduced in December, March, and June also experienced a similar period of first mortality (Fig. 1, curves 2,6; 3,7; 4,8). The first real peak of mortality occurred in September. During the winter after the initial summer-through-October mortality period, mortality was very low. A slight mortality occurred in March in the second-year introductions (Fig. 1, curves 5, 6, 8); this preceded by 1 month the major mortality period for these introductions (broken line). The period of high death rate (30-38 per cent) occurred in May and June. In 3 of the 4 first-year introductions (Fig. 1; curves 1, 3, 4 — solid line) the May-June mortality peaks approximately equaled their preceding September-October peaks.

Even though introductions 1 and 5 were exposed 4, 7 and 9 months before introductions 2 and 6, 3 and 7, and 4 and 8, respectively, all introductions experienced initial peak mortalities during the following September (Fig. 1). Susceptible oysters introduced in June (introductions 4 and 8) had mortalities in September (3-month exposure) comparable to mortalities in oysters introduced more than 9 months earlier (introductions 1 and 5). Therefore, as far as the first period of mortality is concerned, length of exposure was not as significant as seasonality of introduction.

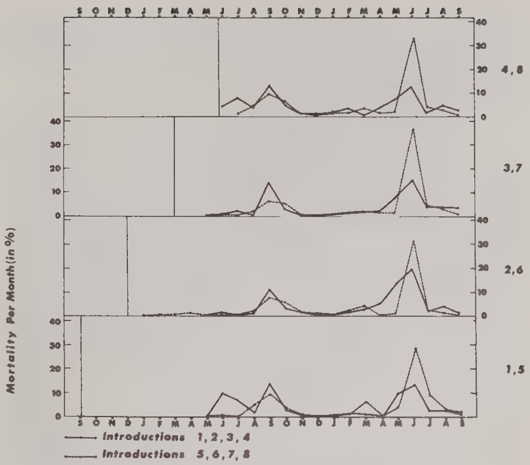

FIG. 1. *Mortality curves for 8 introductions of oysters in Chincoteague Bay, Virginia. Solid line represents introductions 1 through 4. Broken line represents introductions 5 through 8. Vertical scale is in per cent and mortality points are plotted as percentage dead each month of original number of oysters in each introduction.*

Oysters in all introductions had to be exposed to Chincoteague Bay for at least 12 months (i.e. Fig. 1, introductions 4 and 8) before they suffered the peak mortality of May and June. Note that during the first May and June of exposure, mortality was relatively low in most introductions.

Cumulative mortality for each introduction of oysters is given in Table 1. All groups of oysters (except introduction 3) experienced over 70 per cent mortality. It is pertinent that the magnitude of cumulative mortality was not necessarily proportional to the duration of exposure. All introductions experienced approximately similar cumulative mortalities after two summers and one winter of exposure (e. g., compare introductions 1, 5 with 4, 8 in Fig. 1).

INITIAL INCIDENCES AND MONTHLY PREVALENCES OF *MINCHINIA NELSONI*

Initial incidence designates the first appearance of *Minchinia* infections. Prevalence represents the level of infection (percentage of sample infected) in a given introduction at any given time after initial incidence.

Figure 2 shows initial incidences and monthly prevalences for *Minchinia nelsoni* (curves 1-8) and *M. costalis* (histograms) in living oysters. In the first year of introductions, *M. nelsoni* was first observed in March and April in exposed introductions (Fig. 2, introductions 1, 2, 3). These infections consisted of plasmodia largely restricted to the gill and mantle tissues. Initial infections were high in these introductions during these two months. The fourth introduction was made in June.

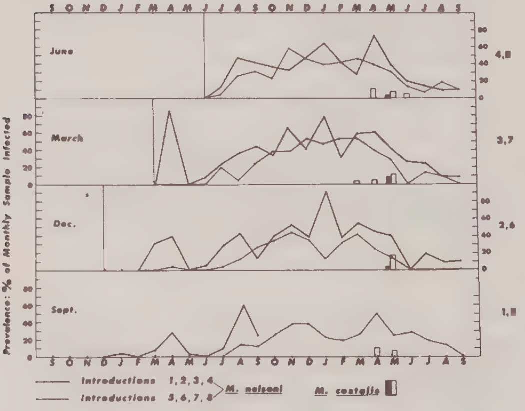

FIG. 2. *Incidence and prevalence data for* Minchinia nelsoni *(lines) and* Minchinia costalis *(histograms). Solid lines and histograms represent prevalences in introductions 1 through 4. Broken lines and stippled histograms represent prevalences in introductions 5 through 8. Vertical scale is in per cent and prevalence is expressed as percentage of sample of oysters infected per month. Note confined seasonal prevalences of* M. costalis *as contrasted to extended prevalences of* M. nelsoni.

In May and June the decrease of the prevalence to a very low level (5 per cent) in the first 3 introductions suggests that the original March-April infections became abortive or that stages of the parasite became cryptic. Prevalences of *M. nelsoni* in introductions 1, 2, 3, and 4 began to rise again in late July and by late August had reached 40 to 60 per cent preceding the first mortality peak in September. A drop in prevalences in 1, 2, and 4 in September possibly reflected infections removed from the introductions by the increased death rate in September. Monthly prevalences of *M. nelsoni* increased during the fall, however, in all introductions [1] and remained moderate to high in most during the winter. The apparent abrupt drop in prevalence during January of the first introduction (Fig. 2) may be a reflection of biased monthly sampling rather than a genuine drop in prevalence.

The high winter prevalence of *M. nelsoni* was not accompanied by any significant mortality (Fig. 1). Prevalence of *M. nelsoni* began to decline in the second spring and remained relatively moderate to low in the subsequent summer months until the end of the study. It should be noted (Fig. 2) that the prevalences of *M. nelsoni* in the spring overlapped the initial incidence of *M. costalis*.

INITIAL INCIDENCES AND MONTHLY PREVALENCES OF *MINCHINIA COSTALIS*

In Figure 2 the solid histograms represent prevalences of *M. costalis* in the first year introductions (1, 2, 3, 4) and the stippled histograms represent prevalences in the second year introductions (5, 6, 7, 8).

The earliest incidence of *M. costalis* was in March (Fig. 2, introduction 7) after a 12-month exposure. Introduction 8 (Fig. 2), however, had initial infection of *M. costalis* in April after only 10 months of exposure. The highest percentages of infections in all introductions occurred in May, after at least 12 months of exposure. In living oysters the apparent prevalences of *M. costalis* were low (highest: 18 per cent, introduction 6, May) in comparison with the prevalences of *M. nelsoni* in the same samples. *Minchinia costalis* was found in oysters only within the time period March to early July. The apparently low prevalences of *M. costalis* in living oysters is probably best explained by the observation that initial infections of the oysters by *M. costalis* slightly preceded and were concurrent with the second peak of mortality (Fig. 1). Apparently many newly infected oysters died quickly (May-June). This idea is supported by the high prevalences of *M. costalis* in dead oysters recovered during May and June from all introductions as discussed in the following section.

PREVALENCE OF *MINCHINIA NELSONI* AND *M. COSTALIS* IN DEAD OYSTERS

Mortalities occurred during warm periods, hence active predators and scavengers (i.e. small crabs and fish) quickly consumed the meats of dying and dead oysters in the trays. Table 2 shows prevalences of the two species of *Minchinia* in dead oysters recoverable during the two heavier mortality periods (these figures are combined data from all 8 introductions). Plasmodial infections of *M. nelsoni* were heavy in most of the oysters that died during September and October. There was much evidence of tissue replacement and damage caused by the plasmodia, particularly in weak and dying oysters. No *M. costalis* infections were found during the September-October mortality.

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[1] Incidence and prevalence data for introduction No. 1 were not determined beyond 1 year of exposure September, 1963, to September, 1964 (See Fig. 2).

TABLE 2. *Prevalences of two species of* Minchinia *in dead oysters during the two peak mortality periods.*

	M. nelsoni	*M. costalis*
Sept.	26/30	——
Oct.	20/24	——
May	14/56	40/56
June	5/63	39/63

Both species of *Minchinia* were found in dead oysters from the May-June period of mortality. Concurrent or double infections with spores of *M. nelsoni* and *M. costalis* in individual oysters were also found during May and June (Couch, 1967): *Minchinia costalis* infections were highest during this early summer mortality. Well over 50 per cent of most of these infections were very heavy and usually occupied every tissue of the host. The prevalence of *M. nelsoni* in dead oysters during May and June was less than that of *M. costalis.* However, the prevalence of *M. nelsoni* was similar in living and dead oysters during May and June (compare Table 2 with Fig. 2).

SPORULATION OF *MINCHINIA NELSONI* AND *M. COSTALIS* IN RELATION TO MORTALITY

Diagnoses of *Minchinia nelsoni* in most cases were based on the identification of plasmodia. Sporulation of *M. nelsoni* has been found infrequently in living oysters and rarely in dying or dead oysters from Chesapeake Bay and Chincoteague Bay (Couch *et al.*, 1966; Couch, 1967). *Minchinia costalis* sporulated regularly, but spores of this species were found mainly in dying or dead oysters during the May-June mortality, and only rarely in living oysters. In the present study over 80 per cent of the diagnoses of *M. costalis* in dying or dead oysters was based upon finding the parasite's characteristic sporocysts and spores whereas almost all of the diagnoses in living oysters containing *M. costalis* were based upon recognition of its plasmodium.

ASSOCIATION OF MORTALITIES WITH *MINCHINIA NELSONI* AND *MINCHINIA COSTALIS*

In most introductions, serious oyster mortality was either preceded by or was concurrent with infections of *Minchinia nelsoni* or *M. costalis* or both (Figs. 1, 2). During the intervals between initial exposure of the oysters and initial incidence of *M. nelsoni,* mortality was not significant (see particularly introductions 1 and 5, Figs. 1, 2). The gradual increase in prevalence of *M. nelsoni* during August and September was concurrent with mortality. On the other hand, the high prevalences of *M. nelsoni* in winter was not accompanied by mortalities. Oysters are at their lowest level of metabolic activity during the winter months because of the lowered water temperatures (Galtsoff, 1964). Thus, even though oysters were heavily infected, it is possible that a potential mechanism of death was not operative until the general metabolism of the host increased with rising spring and summer water temperatures (compare Fig. 3 with Fig. 1). So all of the contributing factors necessary for parasite-induced death were present during the relatively high mortalities of May and June, including initial incidence of a second parasite, *M. costalis.* It is not possible to speculate on the role of salinity. However, salinities were relatively high during periods of mortality (Fig. 3).

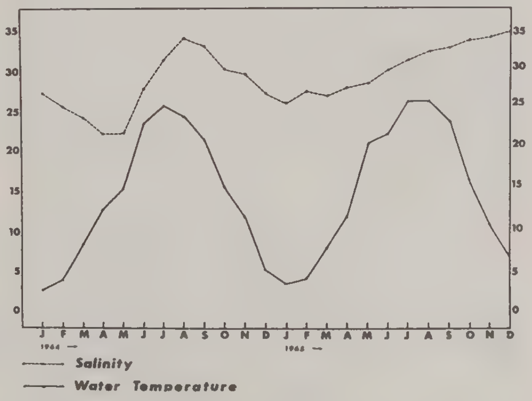

FIG. 3. *Seasonal salinity and temperature curves for Chincoteague Bay, Va. Data used to plot these curves were taken at the dockside tray station, U. S. Bureau of Commercial Fisheries Field Station, Franklin City, Virginia. Each point on the curve represents the average monthly salinity and temperature.*

Depending upon the season of introduction, oysters can become infected within 1 month and apparently mortalities can occur within 3 months (Figs. 1, 2).

It is pertinent to the present discussion to consider another parasite of the oyster that was once indicted as a pathogen, but was later found to have little effect on the host. Prytherch (1940) described *Nematopsis ostrearum*, a gregarine parasite (Eugregarinina: Porosporidae), and thought it was a serious pathogen of oysters. Spores of this parasite are found in tissues of the oyster, which acts as a vector to transmit the parasite to its definitive hosts, mud crabs, when the crabs consume infected oyster tissues. The stages (spores) of the gregarine do not multiply in the oyster. Sprague (1955, p. 102) stated: "Any effect of the parasite on the host must, therefore, be caused by these original invaders; there can be no effect (as in most Sporozoa and in pathogenic bacteria) attributable to multiplication of the parasites within the oyster." Therefore, intensity of infection by spores of *Nematopsis* is directly proportionate to the number of infective stages contacting the oyster, and not to proliferation, or metabolic increase, or activity of the parasite within oyster tissues. The passive spore held within oyster tissues is perhaps less pathogenic than a proliferating parasite that is actively metabolizing and increasing in large numbers. *Minchinia nelsoni* and *M. costalis* appear to have the necessary qualifications for pathogens. Each species apparently increases vegetatively within the oyster; distinct life-history stages are reproduced within the host. Host tissue is replaced drastically by the parasites. Prevalences of the parasites were substantial in living, dying, and dead oysters in epizootic areas during mortality periods. Thus, Andrews' (1966, p. 30) statement, "By reason of a very extensive experience with the distribution of MSX and associated mortalities, it is probable that the first postulate [Koch's], that of regular association, has been satisfied indirectly," is applicable to both *M. nelsoni* and *M. costalis* in Chincoteague Bay.

RELATION OF INFECTION TO REPRODUCTIVE CAPACITY OF OYSTERS

Little has been reported on the influence of haplosporidans on their host's physiology or development. One potentially detrimental effect a parasite may have upon a population is to reduce that population's reproductive capacity by directly or indirectly impeding gametogenesis. Some indirect evidence of this effect is presented in Table 3 for oysters infected with *Minchinia nelsoni* and *M. costalis*. These data were gathered from living oysters sampled from introductions 7 and 8 in April through September, 1966 (main period of gametogenesis) after at least 11 months of exposure. All of these oysters were adults. Before this period (April-September) oysters in these introductions had high prevalences of *M. nelsoni*, and during the period both *M. nelsoni* and *M. costalis* were present in living oysters in each group (Fig. 2).

The essential points to be inferred are: 1) Uninfected oysters (52.3 per cent of total) were most successful in producing gametes (fully developed sperm or eggs); 2) infected oysters were least successful in producing gametes (only 7 per cent), and 3) comparisons between infected and uninfected oysters showed that a slightly higher number of infected oysters were without gonadal development.

It is intriguing to speculate about the history of the gravid, uninfected oysters because the groups from which the above oysters were obtained had a previous high prevalence of *M. nelsoni* and an initial incidence of *M. costalis*. Did these oysters recover from infections in time (before April or May) to begin active gametogenesis? Was there

TABLE 3. *Relationship of* Minchinia *infections and host gonad conditions (1966).*

Months	Uninfected with ripe gonad	Infected with ripe gonad	Uninfected without gonad	Infected without gonad
April	1	1	10	12
May	32	8	12	26
June	22	0	1	4
July	26	2	1	4
August	19	3	6	5
September	12	1	6	0
Totals	112	15	36	51
N=214	52.3%	7.0%	16.8%	23.9%

a genetically controlled resistance mechanism in a certain percentage of the oysters of this group which was activated by physiological changes at the onset of gametogenesis? Had these oysters escaped initial infection completely? The first two questions cannot be answered with presently existing information. The answer to the last question is probably "no", because prevalences of *M. nelsoni* in the source introduction had been so high in the preceding winter as to insure that some of these oysters had been infected at one time.

COMPARISON OF DISEASE IN CHINCOTEAGUE AND DELAWARE BAYS

The patterns of mortality in introduced oysters in Delaware Bay (Haskin *et al.*, 1965) attributed to *Minchinia nelsoni* are, as in Chincoteague Bay, influenced largely by season of introduction rather than duration of exposure. Spring and early-summer introductions have first mortalities in the late summer and early fall of the same year. Late-winter mortalities, reported for Delaware Bay, were not found for oysters in the present study. Late-summer and fall introductions had first mortalities in the following late-winter and June respectively. This timing differs from the September introductions (1, 5) of the present study in that introductions 1 and 5 had first epizootic mortalities in September, 12 months after initial exposure. The sharp June mortality peak reported by Haskin *et al.* (1965) for fall introductions (8 to 10 months of exposure) was not found in Chincoteague Bay for chronologically identical introductions. The June mortalities were attributed to *M. nelsoni* in Delaware Bay, whereas most dead oysters from the June mortalities (12-22 months exposure) were heavily infected with *M. costalis* in Chincoteague Bay. *Minchinia costalis* occurs rarely in Delaware Bay (Haskin *et al.*, 1966) and therefore is probably not a significant cause of mortality there.

Generally the high prevalences of *M. nelsoni* preceding and associated with mortalities in Chincoteague Bay were similar to those in Delaware Bay. Haskin *et al.* (1965) and Haskin (personal communication, 1967) also reported that recently certain high prevalences of *M. nelsoni* in Delaware Bay were not paralleled by heavy mortalities. High winter prevalences of *M. nelsoni* in Chincoteague Bay also were not associated with mortality. The reasons for failure of mortality to coincide with epizootic prevalences of *M. nelsoni* in the two areas at certain times are not understood presently, and are possibly not indentical.

Seasonal mortality peaks in Delaware Bay are apparently higher than comparable peaks in Chincoteague Bay, at Franklin City, Virginia. Spring introductions in Delaware Bay lose from 65 to 85 per cent of the oysters by November (7 — 10 months of exposure) (Haskin *et al.*, 1965). These losses are higher than experienced by any single introduction in Chincoteague Bay during a comparable time period.

COMPARISON OF DISEASE IN CHINCOTEAGUE AND LOWER CHESAPEAKE BAYS

Andrews (1967) pointed out that after 8 years of high prevalences of *Minchinia nelsoni* in lower Chesapeake Bay, there seemed to be no sign that this parasite was diminishing in either prevalence or virulence. The same conclusion apparently held for both *Minchinia nelsoni* and *M. costalis* in Chincoteague Bay as late as 1966 (present study).

As in Delaware and Chincoteague Bays, patterns of oyster mortality attributed to *M. nelsoni* in lower Chesapeake Bay depended more on season of introduction than on duration of exposure (see Andrews, 1966, Figs. 3, 7, 8). Oysters introduced in early spring had first epizootic mortalities in September and October, second mortality in late winter (February), and heaviest mortality in June through October of the second year of exposure. This sequence was similar to that of mortalities in comparable introductions in Chincoteague Bay (Fig. 1) with the following exceptions: 1) Certain seasonal mortalities (i.e. September) in Chesapeake Bay were slightly higher than comparable mortalities in Chincoteague Bay; 2) the late-winter mortality in Chesapeake Bay did not occur in Chincoteague Bay (at least not to a recognizable degree, and 3) the second summer mortalities (Andrews, 1966. Fig. 7) were spread over a longer period (June-September) than those in Chincoteague Bay (May-July).

Slight differences in times of initial incidences of *M. nelsoni* have been found for lower Chesapeake and Chincoteague Bays. Initial infections in lower Chesapeake Bay usually occurred in May (Andrews, 1966), whereas in the present study the majority of initial infections came in late July and August (Fig. 2), except for the possible atypical aborted infections in introductions 1, 2, and 3.

A 2-year prevalence pattern for *M. nelsoni* in epizootic areas of lower Chesapeake Bay was presented by Andrews (1966, Fig. 8). These data can be compared with Figure 2 in the present study in Chincoteague Bay. Andrews presented an extrapolated curve of prevalences based on data collected over a 5-year period, whereas in Figure 2 of the present study actual monthly prevalences (percentage infected of 25 oysters per month) are given for 8 introductions. The actual seasonal prevalences determined in the present study do not differ radically from Andrews' curve of prevalence for lower Chesapeake Bay. Minor differences were: 1) The few high (abortive ?) prevalences of *M.*

nelsoni in Chincoteague Bay in March and April were not found by Andrews in newly introduced oysters in lower Chesapeake Bay; 2) winter prevalences of *M. nelsoni* in Chincoteague Bay seemed, on the average, to be higher than in lower Chesapeake Bay, and 3) spring and early summer prevalences of the second year were not as high in Chincoteague Bay as they were in lower Chesapeake Bay. The significance of these similarities and differences may be open to some questions; these studies are not entirely comparable because of differences in location and years of study, ages of oysters introduced, and origin and susceptibility of stocks and perhaps experimental methods.

Cumulative mortalities in the two areas for comparable periods of exposure were closely similar (Andrews, 1966, Table 5; present study, Table 1). *Minchinia costalis* played no known role in lower Chesapeake Bay mortalities, but was found to be a significant contributor to deaths of oysters on Seaside Virginia (Andrews *et al.*, 1962). The mortalities and prevalences attributed to *M. costalis* for Seaside Virginia were essentially duplicated during the present study in Chincoteague Bay, a similar and nearby locale.

PRACTICAL IMPLICATIONS OF THE PRESENT STUDY

Apparently it would be possible to manipulate oysters introduced in Chincoteague Bay to avoid high mortality from haplosporidans. If trayed oysters were to be placed there for relatively short periods to improve their flavor or for fattening, it would be necessary to introduce them in the fall and harvest them before the following June to avoid the September mortality. If losses of from 10 to 30 per cent could be tolerated, oysters should be introduced in the fall (September), maintained through one winter and subsequent summer, and harvested the second winter without exposing them to the second high mortality period in June (Fig. 1). Exposure of oysters for two summers and a winter results in cumulative losses of approximately 70 per cent (Table 1; — also see Shaw, 1966).

Evidence for stocks of oysters resistant to *Minchinia nelsoni* (developed from naturally selected, innately resistant parents) has been reported by Haskin (personal communication, 1967). The present study was not planned to seek or demonstrate resistance in newly introduced oysters. The only suggestion of possible resistance in these oysters was highly indirect and of uncertain significance. The fact that a certain percentage of each introduction did not die (after 2 years of exposure) suggests that some oysters may be less susceptible to the lethal effects of the parasites than others. No observation on the possibility of acquired immunity was made. Until the microecology and host-parasite relationships are better understood, very little can be said definitely about resistance of any kind in the oyster.

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QUELQUES DONNÉES SUR LA BIOLOGIE ET LA BIOMÉTRIE DE LA CREVETTE PENAEIDE PARAPENAEOPSIS ATLANTICA *BALSS DANS LA RÉGION DE POINTE-NOIRE (RÉPUBLIQUE DU CONGO)*

Par A. CROSNIER* et J. P. WISE**

I. **Introduction.**

Parapenaeopsis atlantica est une crevette qui n'a, jusqu'à maintenant, été trouvée que le long de la côte ouest-africaine, du Sénégal à l'Angola. Cette répartition géographique relativement restreinte, jointe au fait que la pêche des crevettes commence seulement à se développer dans les eaux tropicales et équatoriales ouest-africaines, explique sans doute que nous ne possédions pratiquement aucune donnée sur la biologie de cette espèce qui, en certains endroits, est suffisamment abondante pour pouvoir présenter un intérêt commercial.

Afin de commencer à combler cette lacune, il nous a semblé qu'il n'était pas sans intérêt de donner, ci-après, les quelques observations auxquelles nous avons pu nous livrer sur cette espèce, à la faveur des pêches faites dans le cadre des travaux du Centre ORSTOM de Pointe-Noire.

Les pêches, qui nous ont fourni nos données, peuvent être classées en trois groupes :

1° des pêches faites avec une grande senne de plage à cul à mailles de 18 mm [1]. Ces pêches, au nombre de huit au total, ont été effectuées de mai à novembre 1963 et en juin et juillet 1964.

2° des pêches faites, de 1965 à 1967, avec un chalut à poissons en nylon à cul à mailles de 39 mm, sur tout le plateau continental, à des profondeurs très diverses comprises entre 15 et 100 mètres.

3° des pêches faites, avec un chalut à poissons en nylon à cul à mailles de 39 mm doublé extérieurement par une poche à mailles de 25 mm, lors des recherches sur la sélectivité du chalut utilisé par l'« Ombango », navire du Centre de Pointe-Noire, et sur les variations nycthémérales des rendements. Ces recherches ont consisté en douze sorties, codées S.V.N., chaque sortie durant 24 heures et ayant donné lieu à six traits de chalut exécutés au même endroit et dans le temps

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[1] Cette dimension et les suivantes correspondent à la longueur de la maille étirée.

de la façon suivante : un avant le lever du soleil, un après, un à midi, un avant le coucher du soleil, un après et un à minuit.

Sur ces douze sorties, quatre ont été effectuées sur les fonds de 15 mètres, quatre sur les fonds de 40 mètres et quatre sur les fonds de 100 mètres [1].

II. Les conditions hydrologiques et sédimentologiques au large de Pointe-Noire.

On observe chaque année, sur le plateau continental ponténégrin, deux arrivées d'« eaux océaniques » ($T^o < 18^o$ C ; $34,5 < S$ ‰ < 36) qui viennent momentanément remplacer les eaux chaudes, dessalées et superficielles, qui existent en permanence dans la région Est du Golfe de Guinée et que Berrit (1958) a appelé « eaux guinéennes » ($T^o > 24^o$ C ; S ‰ < 35). Il s'ensuit l'existence de quatre saisons, deux froides et deux chaudes, de longueur et d'intensité inégales (d'ailleurs variables dans d'importantes proportions d'une année à l'autre).

Le cycle saisonnier habituel est le suivant :

- de janvier à avril : grande saison chaude,
- de mai à septembre : grande saison froide,
- d'octobre à décembre : petite saison chaude,
- de décembre à janvier : petite saison froide.

Ce cycle n'est bien entendu qu'approximatif et peut, d'une année à l'autre, présenter certaines variations comme le montre la figure 1 qui représente l'évolution, de la surface à 50 mètres de profondeur, des isothermes en fonction du temps, de janvier 1962 à novembre 1963.

Nous complèterons ce bref exposé en précisant que, lorsque les eaux guinéennes existent, on trouve, entre elles et les eaux océaniques, une masse d'eaux intermédiaires, d'épaisseur variable (de 100 à 10 mètres), de salinité élevée (pouvant atteindre 36 ‰) et de température comprise entre 24 et 18° C. Dans cette masse d'eau, la température varie habituellement rapidement avec la profondeur, ce qui revient à dire que les eaux intermédiaires sont le siège d'une thermocline d'où le nom d'« eaux de la thermocline » que leur a donné Berrit (1958).

Quant au plateau continental, large de 55 km, il a un profil très régulier et une pente faible, de l'ordre de 0,2 %. Les sédiments qui le couvrent, jusqu'aux fonds de 100 mètres, sont essentiellement vaso-sableux ou vaseux, la fraction sablonneuse diminuant au fur et à mesure que l'on s'éloigne de la côte [2].

III. Observations sur la biologie de *Parapenaeopsis atlantica*.

Répartition bathymétrique et caractères du milieu correspondant.

Au cours de nos diverses pêches, nous avons rencontré *P. atlantica* depuis la côte (mais jamais en lagune) jusqu'à 50 et même parfois 60 mètres de profondeur mais jamais au-delà.

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[1] Nous sommes heureux de pouvoir remercier ici MM. Baudin-Laurencin et Gheno à qui nous devons les échantillons des S.V.N. et M. Daget qui a revu notre manuscrit et nous a indiqué de nombreuses modifications à y apporter.

[2] Pour des données plus précises sur la sédimentologie du plateau continental, consulter Poinsard et Troadec (1967), pp. 75-77.

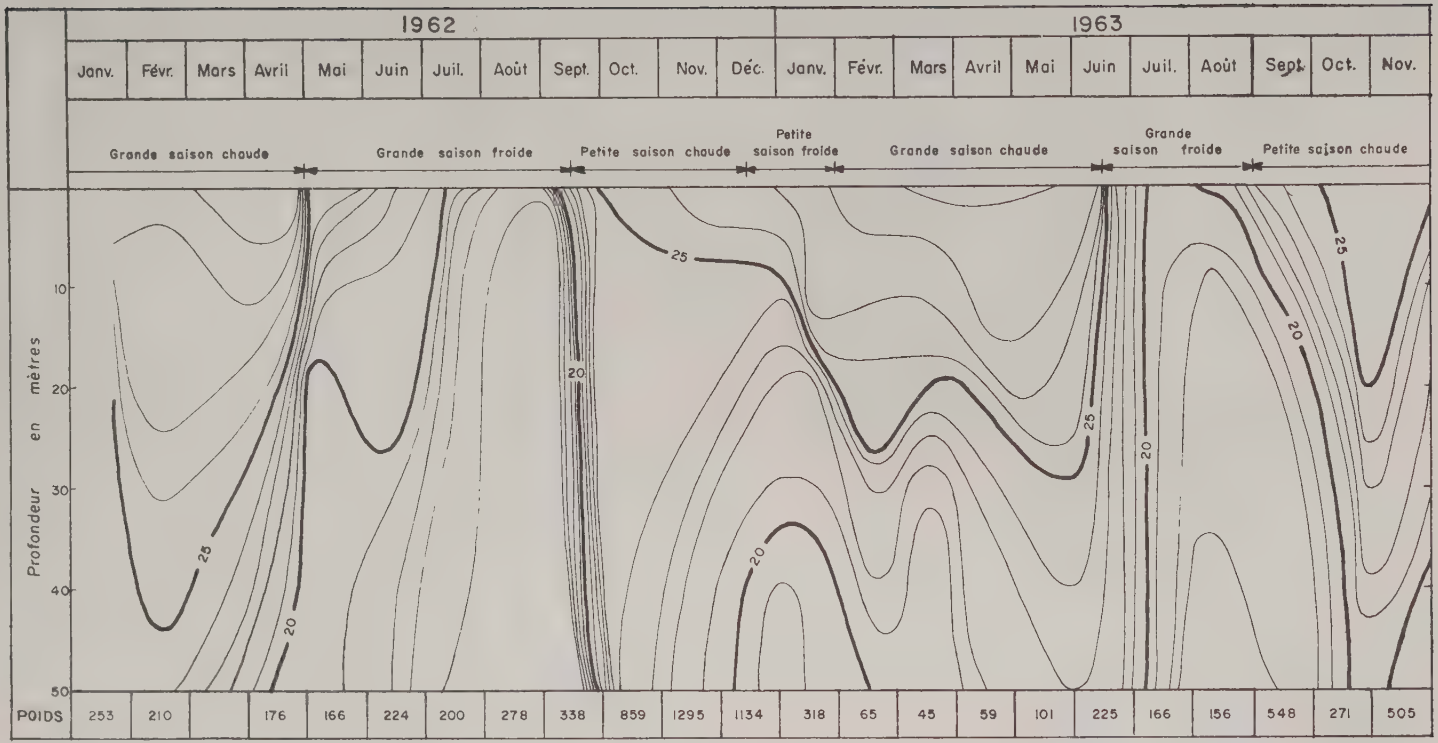

FIG. 1. — Variation des températures, au large de Pointe-Noire, au-dessus des fonds de 50 mètres et poids (en kg) de crevettes débarqués.

A ces fonds correspondent, comme nous l'avons vu précédemment, des sédiments vaseux ou vaso-sableux.

Bien que nous manquions de données précises, la répartition bathymétrique citée ci-dessus paraît relativement stable au cours de l'année malgré les changements de saison. Ceci revient à dire que *P. atlantica* fréquente les eaux guinéennes, moins souvent les eaux de la thermocline, rarement mais parfois la zone supérieure des eaux océaniques[1]. Ceci revient encore à dire que *P. atlantica* se trouve dans des eaux de température toujours au moins égale à 16° C et souvent beaucoup plus élevée (jusqu'à 29° C), la salinité de ces mêmes eaux pouvant être comprise entre 32 et 36 ‰.

D'après les résultats des S.V.N., il semblerait que la densité de la population de *P. atlantica* ne varie guère entre 15 et 40 mètres comme le montre le tableau 1.

L'influence de la saison ne doit pas intervenir dans ces résultats, sauf dans le cas de la S.V.N. 2 qui a été faite en pleine saison froide, alors que toutes les autres ont eu lieu en période de transition (passage de la saison froide à la saison chaude).

Tableau 1. — RENDEMENTS HORAIRES MOYENS EN NOMBRE DE CREVETTES OBTENUS LORS DES S.V.N.

S.V.N.	Profondeur (m)	Date	Nombre d'heures de chalutage	Rendement horaire moyen en nombre de crevettes
11	15	26-27/10	5	843
12	15	28-29/10	5	627
13	15	3-4/11	5	698
14	15	5-6/11	5	579
2	40	31/8-1/9	4	494
9	40	30/9-1/10	6	776
10	40	21-22/10	5	644

Les résultats des assez nombreuses pêches faites sur le plateau continental en dehors des S.V.N. semblent indiquer toutefois, pour l'ensemble de l'année, des rendements maximaux en poids (seule mesure alors relevée) s'obtenant surtout dans la zone comprise entre 15 et 30 mètres de profondeur ; au delà les rendements paraissent décroître plus ou moins doucement jusqu'à 40 mètres, très rapidement ensuite. Une répartition a peu près semblable paraît avoir été observée en Côte d'Ivoire (TROADEC, 1968).

RÉPARTITION DES TAILLES EN FONCTION DE LA PROFONDEUR.

Nous avons analysé les données obtenues avec la senne de plage et, lors des S.V.N., avec le chalut à poissons gréé avec une double poche extérieure.

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[1] Durant la S.V.N. 2 où 4 traits d'une heure ont fourni 1.978 crevettes, la température n'était que de 16,2° C. D'un autre côté, l'influence bénéfique de l'élévation de la température de l'eau sur les rendements est montrée par les résultats de la S.V.N. 9. Durant cette S.V.N., une arrivée d'eau chaude vers 23 h. 00 a fait monter la température de 17,5° à 20,7° C, le rendement horaire moyen calculé sur 3 heures de trait est alors passé de 503 à 1.050 crevettes.

La figure 2 montre les résultats obtenus.

Pour interpréter les courbes, il faut toutefois se souvenir que :

— la senne, à mailles de taille moindre, doit mieux retenir les petites crevettes,

— les courbes données pour les captures faites avec la senne rassemblent des pêches effectuées à des moments très divers de l'année (de mai à novembre), au contraire les pêches faites sur les fonds de 40 mètres ont toutes eu lieu entre le 31 août et le 22 octobre, celles faites sur les fonds de 15 mètres entre le 26 octobre et le 6 novembre.

Ceci posé, il semble bien ressortir des courbes de la figure 2 que, dans toute l'aire étudiée, on rencontre des crevettes de presque toutes les tailles, les plus grosses (carapace > 31 mm) ne semblant pas, toutefois, se trouver sur les fonds de 0 à 2 mètres mais étant très abondantes sur les fonds de 15 mètres et vraisemblablement dès quelques mètres de profondeur.

Les petites crevettes (carapace < 15 mm) paraissent nettement plus abondantes sur les très petits fonds qu'un peu au large, mais le phénomène est certainement accentué, sur nos courbes, d'une part par la différence de sélectivité existant, pour les petites tailles, entre la senne et le chalut à double poche, d'autre part par l'étalement dans le temps des captures faites à la senne [1].

TAILLES DES MÂLES ET DES FEMELLES.
VARIATIONS DU SEX-RATIO.

La différence de taille, habituelle chez les crevettes, entre les mâles et les femelles s'observe très nettement chez *P. atlantica.* Les histogrammes et les courbes des figures 2 et 4 le montrent ; on y voit que, si les femelles peuvent avoir une carapace atteignant 37 mm, chez les mâles la taille maximale observée est de 25 mm.

Les proportions des mâles par rapport aux femelles, observées au cours des différentes pêches, figurent dans le tableau 2.

Malgré de très fortes variations d'un trait de chalut à l'autre, l'ensemble des pêches sur fonds de 15 mètres donne un sex-ratio moyen assez voisin de celui obtenu à partir des pêches faites à 40 mètres (78,9 pour 15 mètres et 88,9 pour 40 mètres) et indiquant une nette prédominance des femelles dans les captures. Près de la côte, comme nous l'avons vu précédemment, la proportion d'individus de petite taille est vraisemblablement supérieure à celle existant sur les fonds de 15 à 40 mètres et, comme les mâles sont plus petits que les femelles, une plus grande proportion d'entre eux a dû échapper aux coups de senne. Ceci pourrait expliquer la faible valeur du sex-ratio observé (17,6 pour 0-2 mètres). La connaissance des courbes de sélectivité des différents engins utilisés serait indispensable pour arriver à une estimation correcte du sex-ratio pour l'ensemble de la popuation.

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[1] Cf. aussi en faveur du décalage de distribution noté, les histogrammes « Senne » et « S.V.N. » de la figure 4 dont certains ont été faits à la même époque de l'année.

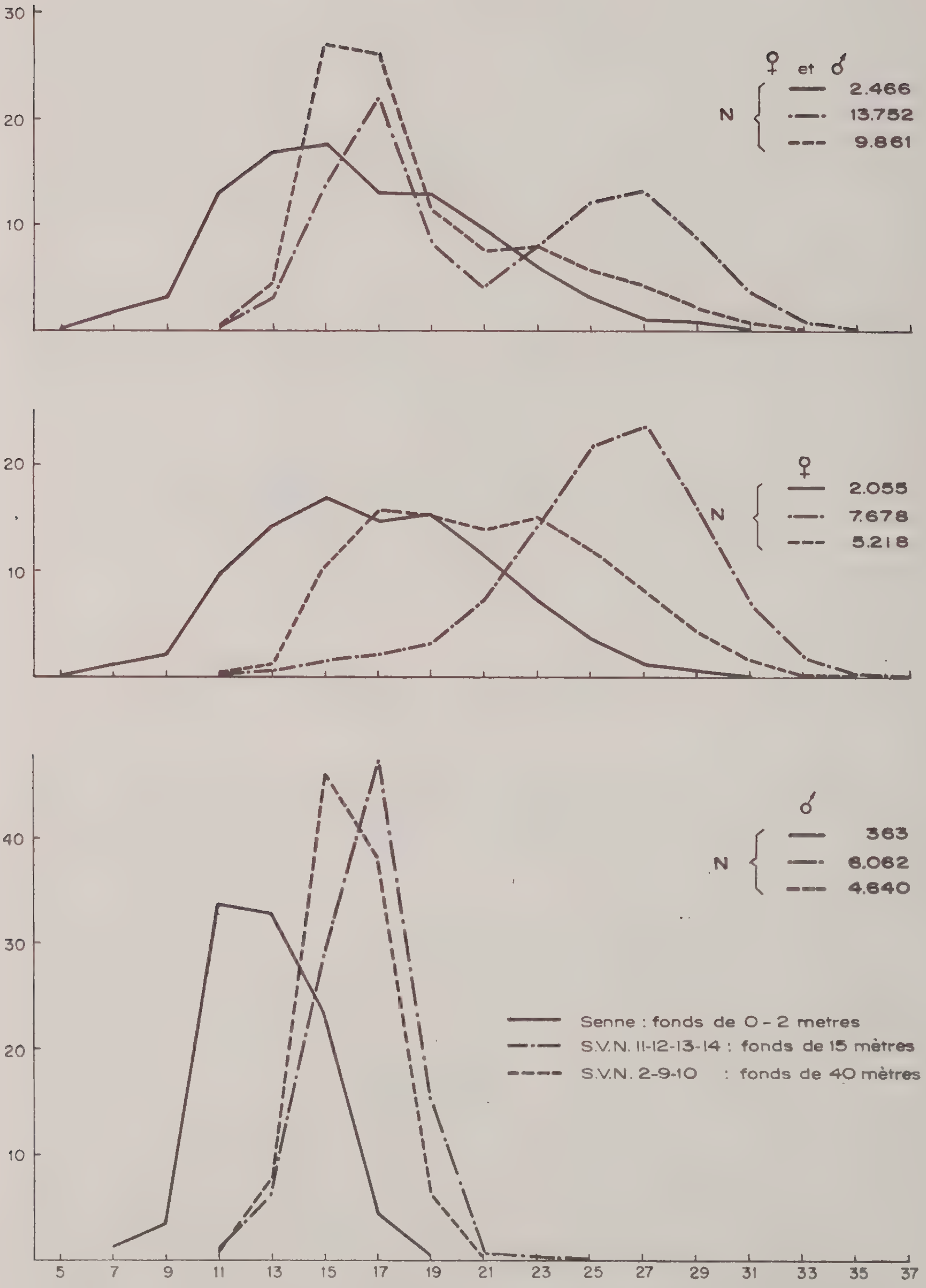

FIG. 2. — Distribution des tailles de *P. atlantica* au-dessus des fonds de 2, 15 et 40 mètres.
En ordonnée : fréquence en pourcentage.
En abscisse : longueur de la carapace en mm.

VARIATION DE LA RÉPARTITION DES TAILLES EN FONCTION DE L'HEURE DE CAPTURE.

Il est intéressant d'essayer de voir si la répartition des tailles varie suivant l'heure de capture, ce qui pourrait avoir pour origine un cycle quotidien, soit de migration bathymétrique soit d'activité, différent suivant les tailles.

Compte tenu du petit nombre d'échantillons dont nous disposons, nous n'avons pu essayer de distinguer une variation qu'entre les traits de jour et les traits de nuit.

Le tableau 3 donne les résultats obtenus sur les fonds de 15 mètres. La similitude de la composition, en pourcentage de taille, des échantillons est frappante et semble bien montrer qu'aucune migration et aucun cycle d'activité différentiels n'existent.

Tableau 2. — SEX-RATIO LORS DES PÊCHES FAITES A LA SENNE ET AU CHALUT A DOUBLE POCHE.

Profondeur		Engin de pêche	Nombre total de spécimens	% ♂/♀
Profondeur	0-2 mètres	Senne	272	9,2
		»	221	21,8
		»	296	10,0
		»	146	15,8
		»	327	20,2
		»	566	29,8
		»	212	25,4
		»	416	8,9
	15 mètres	Chalut à dd. poche	881	111,2
		»	1149	172,2
		»	576	31,8
		»	609	42,2
		»	1004	146,6
		»	623	117,8
		»	616	79,0
		»	621	30,4
		»	647	23,0
		»	640	26,0
		»	567	50,7
		»	406	33,5
		»	760	122,9
		»	812	90,6
		»	946	146,9

Profondeur		Engin de pêche	Nombre total de spécimens	♂/♀
Profondeur	15 mètres	Chalut à dd. poche	337	72,8
		»	468	17,0
		»	378	38,4
		»	876	121,7
		»	836	143,7
	40 mètres	»	517	303,9
		»	695	81,9
		»	70	29,6
		»	696	122,3
		»	1303	144,0
		»	428	18,5
		»	459	13,8
		»	621	19,8
		»	732	48,1
		»	1116	146,3
		»	893	83,7
		»	769	203,1
		»	572	139,3
		»	433	58,0
		»	557	70,5

Tableau 3. — RÉPARTITION DES TAILLES, DE JOUR ET DE NUIT, AU-DESSUS DES FONDS DE 15 MÈTRES.

Longueur de la carapace (mm)	♂ et ♀				♀				♂			
	Nombre de spécimens		Fréquence en %		Nombre de spécimens		Fréquence en %		Nombre de spécimens		Fréquence en %	
	Jour	Nuit	Jour	Nuit	Jour	Nuit	Jour	Nuit	Jour	Nuit	Jour	Nuit
10-12	15	47	0,3	0,6	3	11	0,1	0,2	12	36	0,4	1,1
12-14	178	244	3,2	3,3	21	37	0,7	0,8	157	207	6,5	6,7
14-16	753	952	13,8	13,0	51	62	1,6	1,4	702	890	29,1	29,1
16-18	1183	1571	21,8	21,4	54	104	1,7	2,4	1129	1467	46,8	47,9
18-20	480	554	8,8	7,5	98	108	3,2	2,5	382	436	15,8	14,2
20-22	254	305	4,6	4,1	229	282	7,5	6,6	25	21	1,0	0,6
22-24	419	616	7,7	8,4	418	616	13,8	14,4	1			
24-26	648	949	11,9	12,9	648	949	21,4	23,3				
26-28	715	1018	13,1	13,9	715	1018	23,6	23,9				
28-30	486	664	8,9	9,0	486	664	16,1	15,6				
30-32	215	304	3,9	4,1	215	304	7,1	7,1				
32-34	65	86	1,1	1,1	65	86	2,1	2,0				
34-36	13	12	0,2	0,1	13	12	0,4	0,2				
36-38	1	1	—	—	1	1	—	—				
Total	5425	7323			3017	4254			2408	3057		

VARIATIONS DES RENDEMENTS DE LA PÊCHE AU CHALUT.

A) *Variations saisonnières.*

Sur la figure 1 nous avons noté les captures de crevettes commercialisées, de janvier 1962 à novembre 1963, par un armement de la place. Ces captures sont composées, pour la presque totalité, par *P. atlantica*, sauf de juin à août où elles renferment une faible proportion de *Penaeus duorarum.*

Les poids débarqués ne présentent pas de variations très significatives au cours de l'année sauf de septembre-octobre à décembre où ils sont en nette augmentation. En comparant, comme cela a été fait sur la figure 1, les poids de crevettes débarqués et les variations de la température de l'eau au-dessus des fonds, on constate que l'augmentation notée correspond très exactement à la petite saison chaude. Ce phénomène, dont nous ignorons actuellement la cause, a également été observé en Côte d'Ivoire (TROADEC, 1968).

B) *Variations nycthémérales.*

La figure 3 donne une représentation synoptique, faite d'après BAUDIN-LAURENCIN (1967), des rendements obtenus au cours des S.V.N. et de la répartition des traits au cours de chaque journée de pêche.

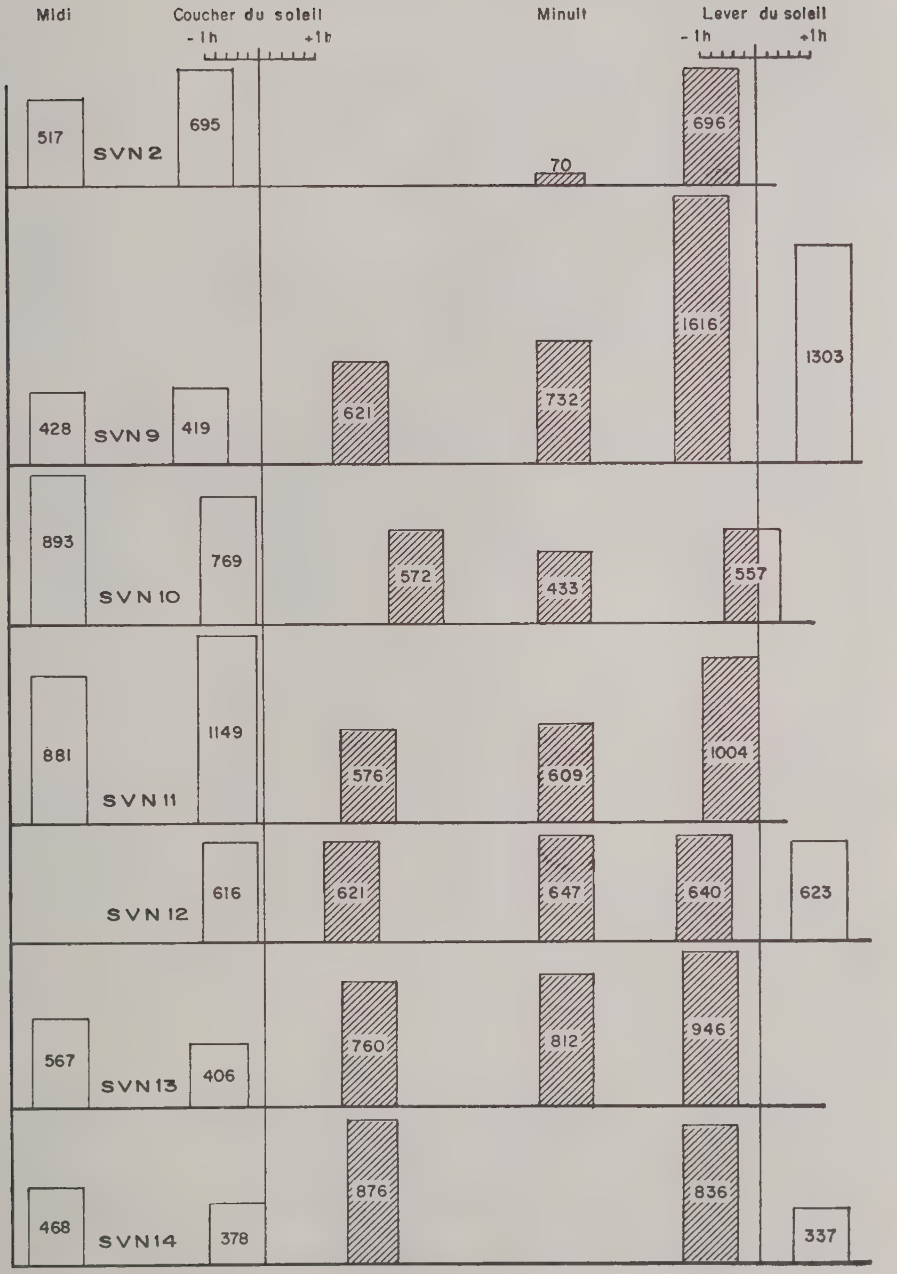

Fig. 3. — Rendements (en nombre d'individus) obtenus au cours des S.V.N. et répartition des traits au cours de la journée.

S.V.N. 2 : 40 m, 31 août-1er sept. — S.V.N. 9 : 40 m, 30 sept.-1er oct. — S.V.N. 10 : 40 m, 21-22 oct. — S.V.N. 11 : 15 m, 26-27 oct. — S.V.N. 12 : 15 m, 28-29 oct. — S.V.N. 13 : 15 m, 3-4 nov. — S.V.N. 14 : 15 m, 5-6 nov.

Sur cette figure, les hauteurs des rectangles sont proportionnelles aux prises (en nombre d'individus), les bases, toutes égales, représentent le temps de chalutage (une heure).

Les rectangles, correspondant aux pêches effectuées aux environs de midi et minuit, sont placés arbitrairement suivant les besoins de la représentation ; ceux correspondant aux pêches effectuées avant et après le lever et le coucher du soleil sont disposés de part et d'autre de verticales, à des distances proportionnelles au temps séparant les traits de chalut du lever et du coucher du soleil.

Ce tableau porte sur un trop petit nombre de chalutages pour que l'on puisse espérer arriver à des conclusions bien valables. On peut surtout remarquer que, d'une façon générale, les rendements sont le plus souvent très variables (la S.V.N. 12 faisant exception) et que la pêche semble pouvoir se faire aussi bien de jour que de nuit, les rendements moyens de nuit étant toutefois, peut-être, légèrement supérieurs à ceux de jour (725 contre 655 pour l'ensemble des chalutages).

Signalons enfin, toujours dans le chapitre des variations nycthémérales, que lors des trois S.V.N. pour lesquelles nous avons les résultats de deux traits encadrant l'aube, celui qui la précède a été plus productif que celui qui la suit. Le phénomène a déjà été signalé à plusieurs reprises pour d'autres espèces, la fin de la nuit semblant amener un regain d'activité chez beaucoup de crevettes.

Vitesse de croissance.

La figure 4 donne les histogrammes des échantillons récoltés avec des filets à petites mailles (senne et chalut à double poche).

Seules certaines séries de ces histogrammes, en particulier celles qui résultent de pêches suffisamment espacées dans le temps et pour lesquelles la distribution initiale n'a pas été trop masquée par des arrivées prolongées de jeunes, paraissent utilisables pour un essai d'évaluation de la vitesse de croissance.

Le tableau 4 indique les séries d'histogrammes retenues pour les mâles d'une part et les femelles de l'autre. La croissance des femelles, qui ont une distribution de tailles plus étalée, a été plus facile à suivre ; en particulier la série des pêches à la senne faites en septembre, octobre et novembre 1963 fournit de bons éléments, une arrivée importante de jeunes, peu étalée dans le temps, s'étant produite en septembre.

Les distributions étant visiblement unimodales, les croissances ont été calculées au moyen de la moyenne arithmétique des échantillons et estimées graphiquement en suivant le déplacement du mode. L'évaluation ainsi obtenue est faussée du fait que nous ignorons la sélectivité de la senne et que les moyennes arithmétiques calculées sont certainement supérieures aux moyennes réelles, et ceci d'autant plus que les échantillons sont formés d'individus de plus petite taille. Il en est de même en principe du mode, mais ici le mode à 10 mm des coups de senne du 10 mai et du 9 septembre est si marqué qu'il semble bien correspondre à la réalité. Il s'ensuit que, dans le cas qui nous intéresse, l'appréciation de la croissance par le mode doit donner une meilleure approximation que celle faite par la moyenne.

La croissance mensuelle moyenne de la longueur de la carapace pourrait donc être évaluée à 2,5 mm pour les femelles dont la carapace a une taille com-

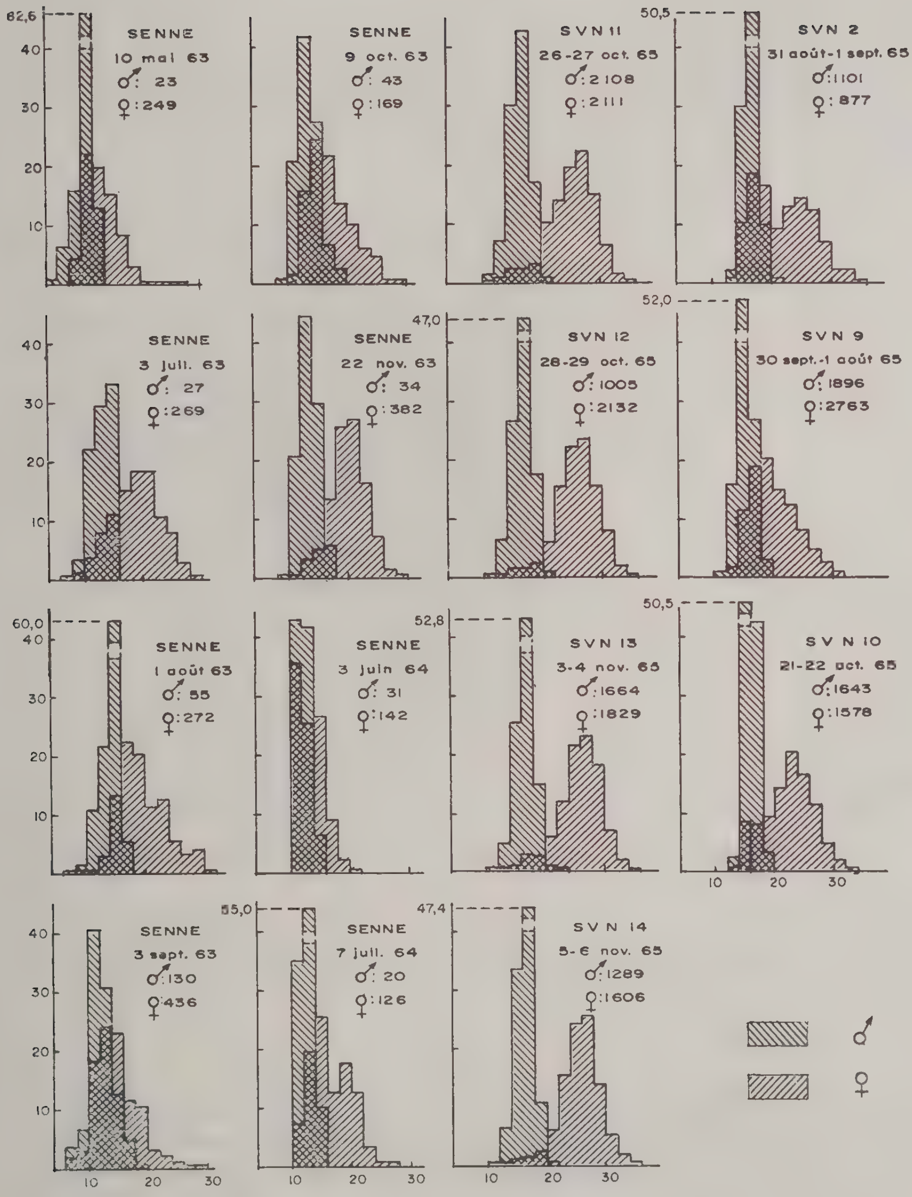

FIG. 4. — Histogrammes des échantillons récoltés à la senne et au chalut à double poche.
En ordonnée : fréquence en pourcentage.
En abscisse : longueur de la carapace en mm.

prise entre 10 et 20 mm et 1,5 mm pour les mâles dont la carapace mesure de 10 à 16 mm, ce qui correspond à une augmentation mensuelle de la longueur totale d'environ 11,5 et 7mm [1]. Ces chiffres ne sont bien entendu qu'approximatifs. La vitesse de croissance doit en effet varier d'une part avec la taille des individus, même dans les limites que nous avons données, la courbe de croissance étant asymptotique, d'autre part avec la température de l'eau, température qui, dans la région de Pointe-Noire, à la côte, peut osciller entre 17 et 30° C.

Tableau 4. — VITESSE DE CROISSANCE.

Date de la pêche	Nombre de jours séparant la pêche de la précédente	Croissance de la carapace depuis la pêche précédente				Croissance mensuelle de la carapace			
		calculée d'après la moyenne arithmétique (mm)		estimée d'après le mode (mm)		calculée d'après la moyenne arithmétique (mm)		estimée d'après le mode (mm)	
		♀	♂	♀	♂	♀	♂	♀	♂
10 mai 1963	—	—	—	—	—	—	—	—	—
3 juil. 1963	55	4,9	2,4	6	3	2,7	1,3	3	1,6
3 sept. 1963	—	—	—	—	—	—	—	—	—
9 oct. 1963	36	2,5	1,4	3	2	2,1	1,2	2,5	1,6
22 nov. 1963	44	2,8	—	4	—	1,9	—	2,7	—
3 juin 1964	—	—	—	—	—	—	—	—	—
7 juil. 1964	44	3,1	—	4	—	2,1	—	2,7	—

IV. Observations biométriques sur *Parapenaeopsis atlantica*.

RELATION ENTRE LA LONGUEUR DE LA CARAPACE ET LA LONGUEUR TOTALE.

La seule mesure précise et commode pour caractériser la taille d'une crevette est la longueur de sa carapace, mesurée du bord postérieur au fond de l'orbite. La mesure de la longueur totale, de la pointe du rostre à l'extrémité du telson, est en effet à proscrire car elle ne peut être relevée que sur des spécimens intacts, or lors des pêches faites au chalut beaucoup de crevettes ont leur rostre cassé, et est sujette à d'assez grandes variations suivant la façon dont l'abdomen est étiré lors de la mesure.

Si la longueur de la carapace est la seule mesure précise et commode possible, il est cependant utile d'établir la relation existant entre la longueur de la carapace LC et la longueur totale LT.

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[1] Voir le chapitre IV de la présente note.

Cette relation, dans le cas de *P. atlantica*, peut s'exprimer de façon satisfaisante par l'équation :

$$LT = - 8{,}351 + 5{,}935\ LC - 0{,}043\ LC^2$$

établie à partir de 502 observations et où LT et LC sont exprimées en millimètres. Cette équation donne une estimation correcte, à 3 millimètres près, de la longueur totale en fonction de la longueur de la carapace.

On voit que la carapace croît un peu plus rapidement que la longueur totale. Cette allométrie est vraisemblablement en liaison avec le fait que la surface respiratoire des branchies, logées sous la carapace, croît en liaison avec le volume du corps et non pas avec la longueur totale.

RELATION ENTRE LA LONGUEUR TOTALE ET LE POIDS TOTAL « P ».

Les équations des droites de régression de log P en log LT ont été calculées pour les mâles, les femelles, et l'ensemble des deux.

On a obtenu :

$$\text{Mâles : } \log P = - 4{,}570 + 2{,}652 \log LT$$
$$\text{avec } N = 148 \quad r = 0{,}980$$
$$\text{Femelles : } \log P = - 4{,}915 + 2{,}848 \log LT$$
$$\text{avec } N = 354 \quad r = 0{,}990$$
$$\text{Mâles et femelles : } \log P = - 4{,}944 + 2{,}861 \log LT$$
$$\text{avec } N = 502 \quad r = 0{,}991.$$

Tableau 5. — RELATIONS TAILLE/POIDS CHEZ *Parapenaeopsis atlantica.*

Longueur de la carapace (mm)	Longueur totale (mm)	Poids total (g)	Poids de la queue (g)
8.0	36	0.4	0.3
8.5	39	0.5	0.3
9.0	42	1	0.4
9,5	44	1	0.4
10.0	47	1	0.5
10.5	49	1	1
11.0	52	1	1
11.5	54	1	1
12.0	57	1	1
12.5	59	1	1
13.0	62	2	1
13.5	64	2	1
14.0	66	2	1
14.5	69	2	1
15.0	71	2	1
15.5	73	2	2
16.0	76	3	2
16.5	78	3	2

Longueur de la carapace (mm)	Longueur totale (mm)	Poids total (g)	Poids de la queue (g)
17.0	80	3	2
17.5	82	3	2
18.0	85	4	2
18.5	87	4	2
19.0	89	4	3
19.5	91	5	3
20.0	93	5	3
20.5	95	5	3
21.0	97	6	3
21.5	99	6	4
22.0	101	6	4
22.5	103	7	4
23.0	105	7	4
23.5	107	7	4
24.0	109	8	5
24.5	111	8	5
25.0	113	9	5
25.5	115	9	5
26.0	117	9	6
26.5	119	10	6
27.0	121	10	6
27.5	122	10	6
28.0	124	11	7
28.5	126	12	7
29.0	128	12	7
29.5	129	13	8
30.0	131	13	8
30.5	133	14	8
31.0	134	14	8
31.5	136	15	9
32.0	137	15	9
32.5	139	16	9
33.0	141	17	10
33.5	142	17	10
34.0	144	18	10

Dans ces équations P est exprimé en grammes et LT en millimètres. N est le nombre d'observations, r le coefficient de corrélation.

Les écarts-types n'ont pas été calculés. Pour la dernière équation, si l'on compare graphiquement les poids observés pour les diverses longueurs et les poids théoriques correspondants calculés d'après la dernière équation (mâles et femelles), on peut admettre que celle-ci exprime de façon très satisfaisante la relation étudiée pour les spécimens dont la longueur totale ne dépasse pas 120 mm, au delà l'erreur peut atteindre un gramme.

Relation entre la longueur totale et le poids de la queue « PQ ».

Trois équations ont également été établies suivant les mêmes principes que pour le poids total.

On a obtenu :

Mâles : $\log PQ = -4{,}583 + 2{,}555 \log LT$
avec $N = 148 \quad r = 0{,}939$.
Femelles : $\log PQ = -4{,}982 + 2{,}773 \log LT$
avec $N = 354 \quad r = 0{,}988$
Mâles et femelles : $\log PQ = -4{,}941 + 2{,}752 \log LT$
avec $N = 502 \quad r = 0{,}989$.

De même que dans la série précédente, l'équation commune aux mâles et aux femelles est très satisfaisante pour les spécimens mesurant jusqu'à 120 mm, au delà l'erreur peut être d'un demi gramme.

Il convient, en outre, de signaler que toutes les équations ci-dessus sont relatives à des spécimens capturés en mai, juin et juillet et qu'il est possible que les relations taille/poids varient légèrement durant l'année.

V. **Conclusions.**

Malgré leur caractère très fragmentaire, il ressort des différentes observations faites dans la région de Pointe-Noire que *Parapenaeopsis atlantica :*

— est une crevette côtière ne semblant jamais se rencontrer à plus de 60 mètres de profondeur et surtout abondante de 10-15 mètres[1] à 30-40 mètres,

— fréquente surtout les eaux chaudes mais peut, au moins à certaines époques de l'année (saison froide), se trouver dans des eaux ne dépassant pas 16° C,

— se trouve sur les fonds vaseux ou vaso-sableux,

— effectue sa croissance entièrement en mer et ne pénètre jamais dans les lagunes,

— ne présente pas de répartition bathymétrique très nette en fonction de la taille, bien que les petites tailles soient mieux représentées à la côte qu'au large,

— ne paraît pas présenter de répartition bathymétrique différente pour les mâles et les femelles,

— a une croissance mensuelle moyenne qui peut être évaluée, en augmentation de longueur de la carapace, à 2,5 mm pour les femelles dont la carapace a une taille comprise entre 10 et 20 mm et 1,5 mm pour les mâles dont la carapace mesure de 10 à 16 mm, ce qui correspond à une augmentation de la longueur totale de 11,5 et 7 mm.

Du point de vue des rendements de la pêche au chalut on note :

— des rendements maximaux, semble-t-il, durant la petite saison chaude,

— une grande variabilité dans les rendements au cours d'une même journée,

— l'absence de prédominance nette entre les rendements de jour et ceux de nuit.

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[1] Williams, dans le rapport du Guinean Trawling Survey, signale *P. atlantica* à plusieurs reprises jusqu'à 200 mètres de profondeur ; il s'agit, sans aucun doute, d'erreurs de détermination, l'espèce ayant vraisemblablement été confondue avec *Parapenaeus longirostris* (Lucas).

Sur le plan de la biométrie, des relations ont été calculées donnant la longueur de la carapace, le poids total et le poids de la queue en fonction de la longueur totale.

Summary.

Incomplete information based on observations made at Pointe-Noire indicates that *Parapenaeopsis atlantica* is a coastal marine shrimp never encountered deeper than 60 meters and most common between 10-15 meters and 30-40 meters. It lives principally in warm water, but may be found at least in certain seasons in water as cold as 16° C. *P. atlantica* inhabits muddy or sandy-mud bottoms, and never occurs in brackish-water lagoons.

This shrimp does not show a clear distribution of sizes with depth, although the smaller sizes may be more abundant closer to shore. There is no clear-cut difference in depth distribution of males and females.

Monthly growth is estimated as 2.5 mm (carapace length) for females with carapace lengths between 10 and 20 mm, and 1.5 mm (carapace length) for male with carapace lenghts between 10 and 16 mm. These values correspond approximately to growth in total length of 11.5 and 7 mm per month. Relations were calculated between carapace length, total length, total weight and weight of the " tail ".

Experimental fishing shows that there is a great variation in catches made the same day in the same area, and that there is no clear-cut difference between day and night catches. From the commercial fishing it would seem that maximum trawl catches are made in the short warm season.

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Distribution of ^{65}Zn In Tissues of Two Marine Crustaceans Determined by Autoradiography[1]

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ABSTRACT

In the benthic amphipod *Anonyx* sp., and the euphausiid *Euphausia pacifica* Hansen, ^{65}Zn accumulated from seawater was shown by autoradiography to be localized predominantly in the exoskeleton and interstitial spaces of the myofibrils. Also, the gut and hepatopancreas of *Anonyx* sp. and the eye of *E. pacifica* contained ^{65}Zn. The presence of ^{65}Zn in crustacean exoskeletons may affect the efficiency of transfer of ^{65}Zn through the food web and the vertical distribution of ^{65}Zn in the Pacific Ocean along the Oregon coast.

INTRODUCTION

We have used the technique of autoradiography to determine the distribution of ^{65}Zn in tissues of the benthic amphipod *Anonyx* sp.[5] and the euphausiid *Euphausia pacifica* Hansen. To date, the study of the distribution of both radioactive and stable elements in tissues of aquatic crustaceans has been limited to the larger decapods (Vinogradov, 1953; Bryan, 1961, 1964, 1965, 1967a; Hiyama and Khan, 1964; Hiyama and Shimizu, 1964; Polikarpov, 1966; Sather, 1966). The methods used by these investigators to describe elemental distribution were the same as those used for fish and mammals, i.e., dissection and analyses of individual body parts. This approach has little applicability to small crustaceans, such as euphausiids and amphipods, because dissection and accurate elemental analyses are extremely difficult. The use of autoradiography, which can be either qualitative or quantitative, allows one, however, to determine the presence of a radionuclide in animal tissue without dissection.

Recently both *Anonyx* sp. and *E. pacifica* have been the subject of laboratory investigations dealing with the metabolism and cycling of ^{65}Zn in the marine environment. Uptake and elimination rates of ^{65}Zn as affected by

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[5] *Anonyx* sp. is a new species and is currently being described by Dr J. Laurens Barnhard of the U.S. National Museum using specimens from our collections.

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food, temperature, and sediment have been determined for *Anonyx* sp. (Cross, MS, 1968; Cross et al., 1968) and similar rates have been determined for *E. pacifica* with regard to temperature and concentrations of ^{65}Zn in sea water (Fowler et al., 1968). The purpose of this paper is to describe the distribution of ^{65}Zn in tissues of *Anonyx* sp. and *E. pacifica* by the use of autoradiography.

METHODS

The experimental animals were captured in neritic waters off the Oregon coast during the summers of 1965 and 1966. The amphipods were collected with baited traps placed on the bottom at depths of 80–120 m, whereas euphausiids were obtained by towing a ½-m net to a depth of 3 m at night. All animals were transported alive to the Battelle Northwest Laboratory in Richland, Washington, where the experiments were conducted.

The two species were held in separate containers at 7–10 C in membrane-filtered (0.45 μ pore size) sea water containing 25 μCi ^{65}Zn/liter and an average concentration of stable Zn of approximately 20 μg/liter. After 8 days in the radioactive water, the animals were removed, preserved in 10% buffered formalin, imbedded in paraffin, and sectioned with a microtome. Autoradiographs were prepared by dipping de-paraffinized slides of the animal tissue into a liquid nuclear tract emulsion (a mixture of equal portions of Ilford K-5 Nuclear Tract Emulsion,[6] in gel form, and distilled water). The slides were then placed in light-tight boxes in a refrigerator at 5 C, and left for about 3 weeks until the emulsion was exposed. The emulsion was developed in Kodak D-19 developing solution, and the slides were stained with haemotoxylin and eosin. This technique is a modification of a method described by Novek (1962).

DISTRIBUTION OF ^{65}ZN IN TISSUES OF *ANONYX* SP.

Autoradiographs of amphipods that accumulated ^{65}Zn from sea water showed that the exoskeleton was a predominant site of localization of ^{65}Zn. The ^{65}Zn in the exoskeleton appeared to have penetrated into the inner layers (Fig. 1A). Zinc-65 was present also in most of the cracks and fissures of the outer portion of the exoskeleton. Thus, a portion of the exoskeleton may be permeable to zinc. Little is known about the crustacean exoskeleton, except that it exhibits varying degrees of permeability to water and salts in the environment (Dennell, 1960).

Another area of high concentration of ^{65}Zn was muscle tissue. Here much of the radionuclide apparently is restricted to interstitial spaces of the myofibrils (Fig. 1B) — an indication that part of the body burden of ^{65}Zn is in the body fluids. This observation agrees with results obtained by Bryan (1964) who found that changes in the concentration of zinc in the muscle of the lobster *Homarus vulgaris* varied with changes in the concentration of zinc in blood located in the extracellular spaces. Also, muscles that can contract quickly have less zinc than slow-contracting muscles, and muscle-to-blood ratios for ^{65}Zn in "slow" muscle are roughly double those for "fast" muscle (Bryan, 1967b). Bryan suggested that "slow" muscle is the more permeable to zinc; if musculature in amphipods is comparable with that in decapods, the muscle of *Anonyx* sp. in Fig. 1B may be fast-contracting muscle because very little ^{65}Zn has penetrated into the muscle tissue.

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[6] Trade names referred to in this publication do not imply endorsement of commercial products.

Some ^{65}Zn was present in the gut (Fig. 1C) and in the hepatopancreas (Fig. 1D). Because ^{65}Zn was accumulated directly from filtered sea water by the amphipods, the presence of this radionuclide in the gut could not be due to absorption from radioactive food, unless bacteria were available as a source of nutrition. If *Anonyx* sp. swallows sea water, the presence of ^{65}Zn in the gut would not be surprising. Bryan (1964) stated that when the lobster *H. vulgaris* was exposed to sea water of high stable zinc content (100 μg per liter), much of the accumulated zinc was taken up in the hepatopancreas but very little by the gut. Comparison of our data with Bryan's may not be completely valid because the lobsters he used were exposed to sea water longer (15–43 days) than the exposure period for *Anonyx* sp. (8 days).

DISTRIBUTION OF ^{65}ZN IN TISSUES OF *EUPHAUSIA PACIFICA*

The distribution of ^{65}Zn in exoskeleton and muscle tissue of *E. pacifica* was similar to that already described for *Anonyx* sp., i.e., ^{65}Zn was present on the outer surface of the exoskeleton (Fig. 2A) and in the interstitial areas around the myofibrils (Fig. 2B). The musculature shown in Fig. 2B, from the dorsal cephalothoracic region, contained small amounts of ^{65}Zn, and might be "fast" muscle. Fowler et al. (1968) reported that body fluids lost during dissection of internal tissues of euphausiids accounted for about 17% of the total body burden of ^{65}Zn.

Autoradiographs gave no evidence of ^{65}Zn in the gut of euphausiids. The canals of the hepatopancreas, however, showed some traces of ^{65}Zn (Fig. 2C) which might have entered there via the gut, or by absorption from the blood after absorption through the gills. It is not known whether *E. pacifica* swallows significant amounts of water.

The eye of *E. pacifica* contained ^{65}Zn along both sides of the cornea and along the outer surface of the lens (Fig. 2D). Zinc-65 has been detected also in the eye of a fin whale, *Balaenoptera physalus* (Osterberg et al., 1964c), and in the eyes of several species of freshwater fish taken from the Columbia River (Watson, 1966). Leiner and Leiner (1944) reported the presence of stable zinc in the eyes of both freshwater and marine fish. Retention of ^{65}Zn in the eyes of *E. pacifica* may be of little quantitative significance, however, because these organs accounted for only 4% of the total body burden in this species (Fowler et al., 1968).

ECOLOGICAL IMPLICATIONS

The distribution of elements in tissues of marine crustaceans may have ecological as well as physiological significance and may affect the efficiency with which the elements are transferred through the food web. Elements sorbed to exoskeletal material might not be as readily assimilated by a consumer as those located in body fluids or bound to muscle or internal organs. Indirect evidence indicates that the method by which ^{65}Zn is accumulated by *Anonyx* sp. and *E. pacifica* affects the fraction of ^{65}Zn associated with the exoskeleton. In experiments measuring elimination rates of ^{65}Zn in *Anonyx* sp., Cross et al. (1968) found that the fraction of the ^{65}Zn lost at molting was about 20% of the total body burden when accumulation had been directly from filtered sea water and only 2% when accumulation had been from food (*Artemia*). Similarly, in *E. pacifica* the loss of ^{65}Zn at molting was about 18% when accumulation was from filtered sea water (Fowler and Small, 1967) and only 1% when accumulation was from ingestion of labeled *Artemia* (S. W. Fowler, L. F. Small, and J. M. Dean, unpublished data). These differences in the loss of ^{65}Zn at molting appear reasonable since accumulation of ^{65}Zn from water should result in a larger fraction of the total body burden sorbed to the exoskeleton than if accumulation had been from food.

Molting by large populations of *E. pacifica* also might play a significant role in the vertical distribution of ^{65}Zn along the Oregon coast. During the summer months this region receives the waters of the Columbia River, which contain significant amounts of ^{65}Zn as a result of the Hanford Atomic Operations plant in Richland, Washington. *Euphausia pacifica* often represents the largest biomass of macroplankton in Oregon coastal waters (Osterberg et al., 1964a) and serves as forage for a variety of marine animals including the lanternfish, *Lampanyctus leucopsarus* (Osterberg et al., 1964b); coho salmon, *Oncorhynchus kisutch* (Kujala et al., 1968); and the baleen whale, *Balaenoptera physalus* (Osterberg et al., 1964c). In addition, *E. pacifica* undergoes diel vertical migrations, ranging from the surface at night to greater than 200 m during the day (Osterberg et al., 1964a), and therefore is available to mesopelagic as well as epipelagic predators. Fowler and Small (1967) postulated that sinking exoskeletons of *E. pacifica* could significantly affect the vertical distribution of ^{65}Zn along the Oregon coast, since these organisms have a molting frequency of about 5 days. Because of the benthic habits of *Anonyx* sp., however, molted exoskeletons of this species would concentrate near the bottom and not affect the vertical distribution of ^{65}Zn.

We have demonstrated that autoradiography is a useful means by which knowledge of elemental distribution can be gained. Although the autoradiographs presented in this study were not analyzed quantitatively, they do give an insight into the relative capacities of various tissues to concentrate ^{65}Zn directly from sea water. If we assume chemical similarity between ^{65}Zn and stable zinc, relative concentrations of the stable isotope in various tissues are also indicated by the method.

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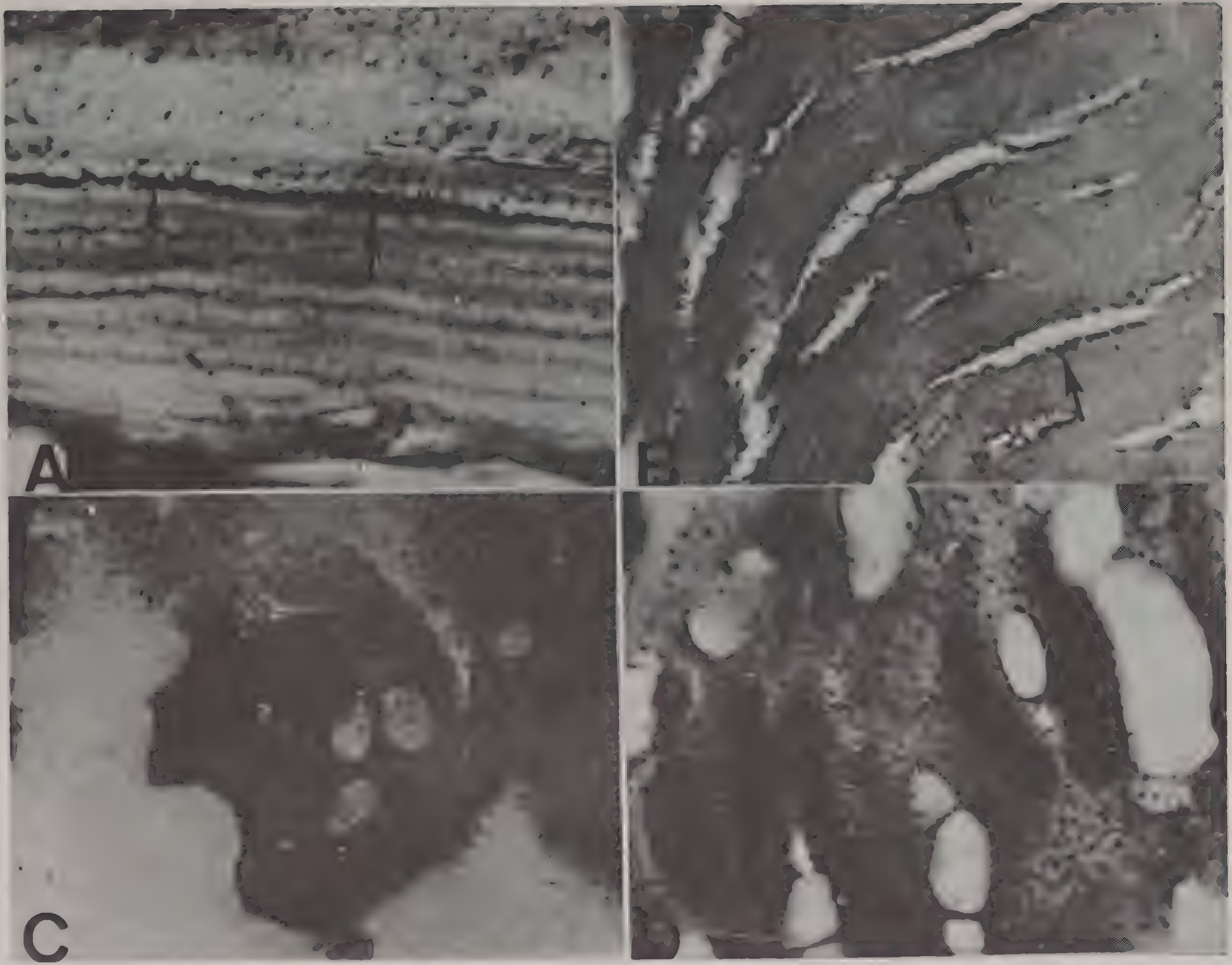

FIG. 1. Autoradiographs (400 ×) showing the presence of ^{65}Zn in *Anonyx* sp. for (A) exoskeleton, (B) muscle, (C) gut, and (D) hepatopancreas. The presence of ^{65}Zn is shown by the darkened areas in the exoskeleton and along the interstitial spaces of muscle (see arrows), and by the scattered black dots in the gut and hepatopancreas.

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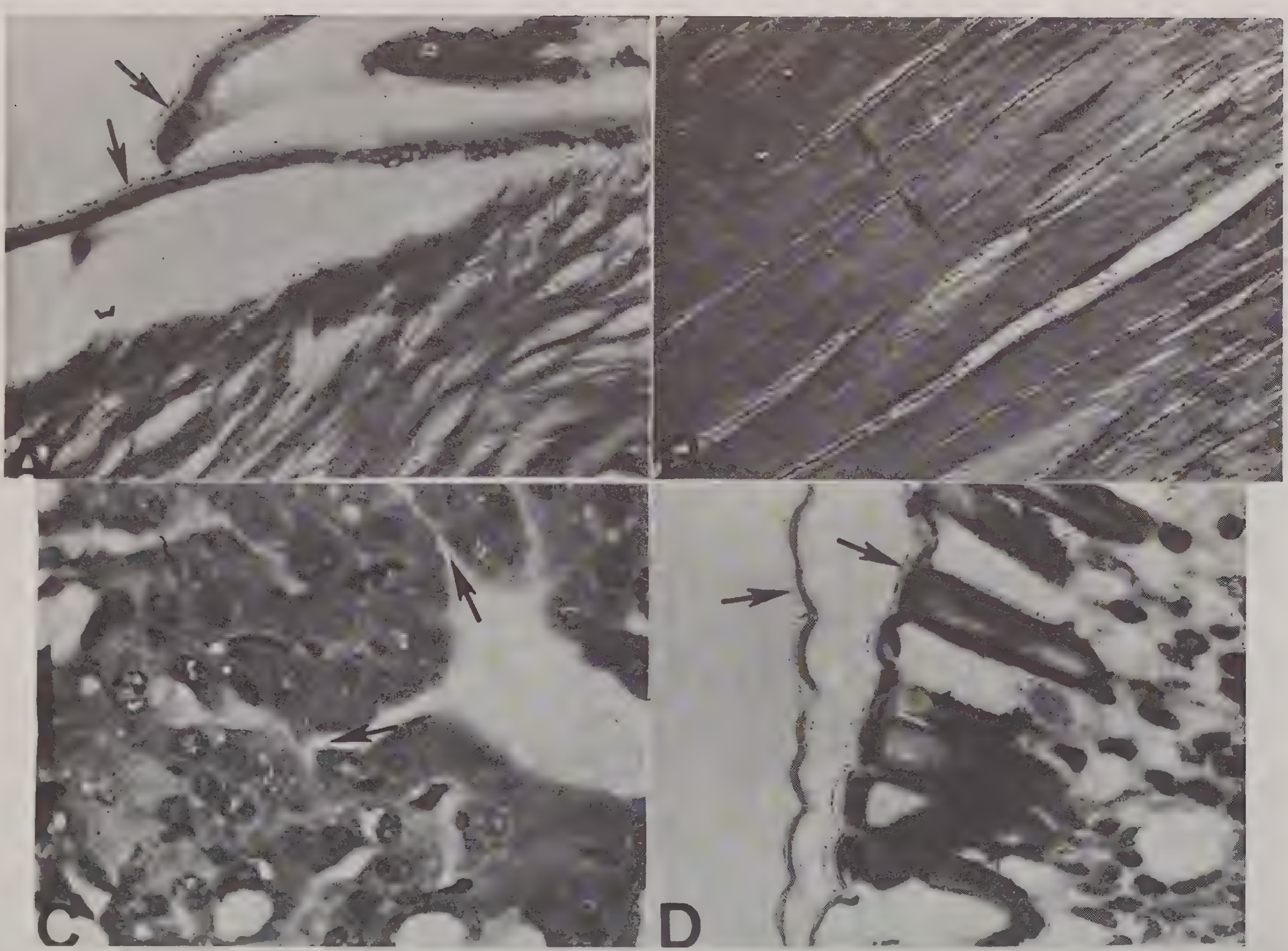

FIG. 2. Autoradiographs (400×) showing the presence of ^{65}Zn in *E. pacifica* for (A) exoskeleton, (B) muscle, (C) hepatopancreas, and (D) eye. Arrows point to areas of localization of ^{65} Zn.

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Species Associations of Benthic Fishes on the Continental Shelf and Slope off Oregon[1]

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ABSTRACT

Four species associations of benthic fishes found off the coast of Oregon within the depth interval from 40 to 1829 m were characterized by two or three most abundant species, depth range, and average sediment type.

Little overlap was found among species associations because many species had maximum abundance or were found only in one association. When a species occurred in more than one association, different sizes of fish were often found. Species on the lower continental slope had the broadest depth range, and a few species were found only in the deepest association.

Sixty-seven species of bottom fishes representing 21 families were collected, but 86% of the total number of fishes were from the families Pleuronectidae, Scorpaenidae, and Bothidae.

INTRODUCTION

Benthos are an important component of the marine ecosystem, and more information is needed on their ecology, species associations, and distributional patterns. This is particularly true in the northeastern Pacific Ocean, where international exploitation of fish stocks has increased much more rapidly than knowledge necessary for effective management of these fisheries (Alverson, et al., 1964).

Until recently, little was known about the depth distribution and species composition of benthic fishes inhabiting the northeastern Pacific Ocean. Grey (1956), for example, stated that no conclusions could be reached on the composition of the deepwater fishes of the eastern Pacific region, because little bottom fishing has been conducted in these waters since the *Albatross* cruises of the late nineteenth and early twentieth centuries.

Trawling surveys in recent years, mainly by the U.S. Bureau of Commercial Fisheries, have greatly increased knowledge about the distribution and abundance of demersal fishes of the northeastern Pacific (Alverson, 1953;

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Hitz and Alverson, 1963; Alverson et al., 1964). Catch data from commercial trawlers have also been used to show seasonal variations in the catch patterns at various depths for some commercially important fishes (Alverson, 1960) and to show the species composition of the Oregon otter trawl fishery (Harry, MS, 1956).

The purpose of this study was to learn if species associations or assemblages of benthic fishes are obvious from an analysis of catch data off the central Oregon coast and, if associations are apparent, to learn how they are related to bottom sediment type and depth of water. This paper is based on a survey of benthic fishes at depths from 40 to 1829 m on the continental shelf and slope off the central coast of Oregon. The continental terrace off Oregon is narrow and steep, extending to 106–109 km from shore (Byrne, 1962; Shepard, 1948). This feature permitted sampling a wide range of depths and sediment types on the shelf and slope within a short distance from shore.

METHODS

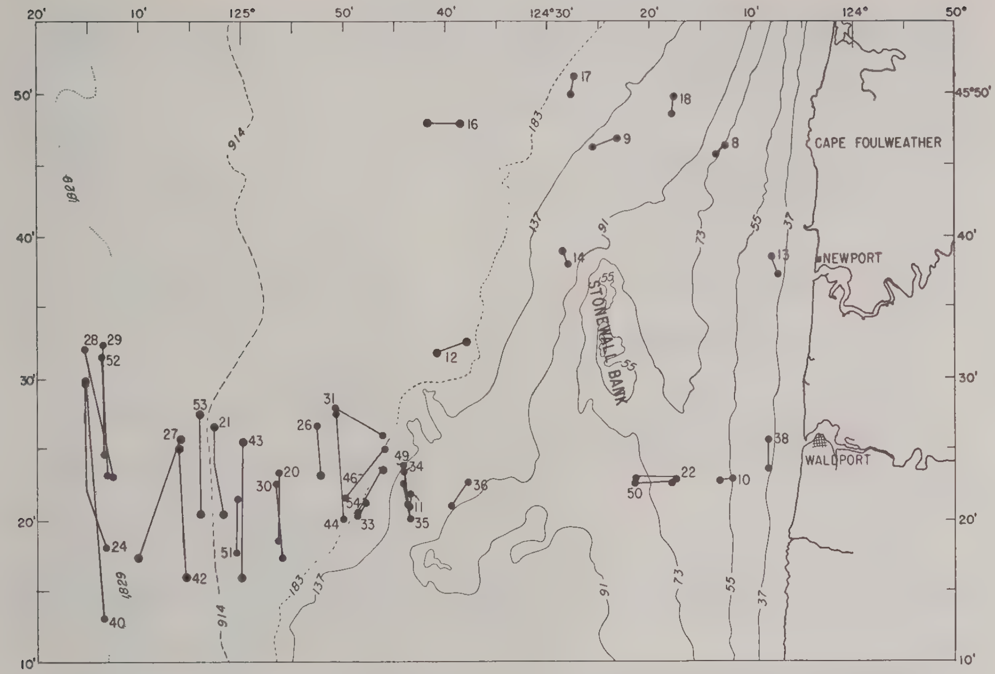
Benthic fishes were sampled with a semi-balloon shrimp trawl (Greenwood, 1959). The headrope of the trawl was 6.7 m long and the footrope 8.2 m long. The net was constructed from 32-mm (stretch measured) cotton netting of number 18 thread. Either wood or metal otter doors were used to spread the trawl.

All tows were made with the single warp method in which a bridle, composed of two 30-m legs of braided nylon rope, connected the otter doors and net to the 9.5-mm towing cable.

The trawl was set and retrieved while the ship was underway at low speeds, and towed at a speed of approximately 3 knots. The duration of each tow, estimated from the time the maximum amount of cable was in the water to the beginning of retrieval, was 20 min where the depth was 274 m or less, and 30–60 min where the bottom was deeper. The amount of cable required to trawl on the bottom was established by trial. A 4:1 to 6:1 ratio of wire length to water depth was used for the stations inshore of the 366-m contour and 2.5:1 or 3:1 for deeper stations. These ratios are similar to those given by Pereyra (1963) for a 13.1-m flat shrimp trawl.

In all, 36 samples were collected off the central Oregon coast from Cape Foulweather to Waldport at depths from 40 to 1829 m (Fig. 1) between July 1961 and June 1962. Fourteen samples were obtained over the shelf (146 m or less) and 22 samples on the slope (146–1829 m).

Station positions were determined primarily by Loran with radar and echo-sounding equipment as supplementary navigational aids. A Precision Depth Recorder in conjunction with an Edo Echo Sounder was used to determine depth and suitable bottom topography. Tows were usually made over comparatively flat terrain parallel to the bottom contour lines. Nevertheless, the trawl was torn or lost during 6 of 12 unsuccessful tows, evidence of the roughness of the bottom in this area. The main obstruction to bottom trawling on the shelf was a region of rock out-cropping known as Stonewall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10'
125°
50'
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20'
10'
124°
50°
50'
40'
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20'
10'
45°50'
40'
30'
20'
10'
1829
914
183
137
91
73
55
37
CAPE FOULWEATHER
NEWPORT
STONEWALL BANK
WALDPORT
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FIG. 1. Location of trawling stations off the central coast of Oregon. The length of the lines indicates the total distance of the tow, including ascent and descent of the trawl.

Bank (Fig. 1). Sampling locations on the shelf were usually on the periphery of this rock formation.

Benthic fishes in the samples were sorted into taxonomic groups and the most abundant species were identified and measured (total length) at sea. The remaining fish were preserved in 10% formalin at sea and identified and measured ashore.

A Dietz-LaFond sampler was used to collect sediment from the continental shelf, and a Phleger corer with a 300-mm sample tube was used on the slope. Sediment samples were collected at each trawl station for particle-size analyses. Hydrometric and settling tube methods were used to determine the percentage composition of sand, silt, and clay (Wentworth scale).

RESULTS

SPECIES COMPOSITION

A total of 7689 fishes representing 21 families and 67 identified species was collected during this study (Table I). Most of these fishes are considered to be benthic or demersal, although some are pelagic and swim just above the bottom; others may migrate vertically and occur near the bottom only during daytime. Midwater fishes, mainly mesopelagic species (see Pearcy, 1964), were collected as the net descended or ascended through the water column but are not included.

TABLE I. List of benthic fishes collected off the central coast of Oregon during this study.

Families and species

- Myxinidae
  - *Eptatretus deani* (Evermann and Goldsborough) 1906
  - *Eptatretus stoutii* (Lockington) 1878
- Squalidae
  - *Squalus acanthias* Linnaeus 1758
- Rajidae
  - *Psammobatis spinosissimus* Beebe and Tee-Van 1941
  - *Raja binoculata* Girard 1854
  - *Raja kincaidii* Garman 1908
  - *Raja rhina* Jordan and Gilbert 1880
  - *Raja trachura* Gilbert 1891
- Chimaeridae
  - *Hydrolagus colliei* (Lay and Bennett) 1839
- Alepocephalidae
  - *Alepocephalus convexifrons* Garman 1899
- Moridae
  - *Antimora rostrata* Gunther 1878
- Gadidae
  - *Microgadus proximus* (Girard) 1854
- Macrouridae
  - *Coryphaenoides acrolepis* (Bean) 1883
  - *Coryphaenoides pectoralis* (Gilbert) 1891
- Embiotocidae
  - *Cymatogaster aggregata* Gibbons 1854
- Bathymasteridae
  - *Ronquilus jordani* (Gilbert) 1888
- Stichaeidae
  - *Plectobranchus evides* Gilbert 1890
- Zoarcidae
  - *Aprodon cortezianus* Gilbert 1890
  - *Bothrocara brunneum* (Bean) 1890
  - *Bothrocara remigera* Gilbert 1915
  - *Embryx crotalina* (Gilbert) 1890
  - *Lycodes diapterus* Gilbert 1891
  - *Lycodopsis pacifica* Collett 1879
- Brotulidae
  - *Cataetyx rubrirostris* Gilbert 1890
- Scorpaenidae
  - *Sebastolobus alascanus* Bean 1890
  - *Sebastolobus altivelis* Gilbert 1893
  - *Sebastolobus* spp.
  - *Sebastodes alutus* (Gilbert) 1890
  - *Sebastodes crameri* Jordan 1896
  - *Sebastodes diploproa* (Gilbert) 1890
  - *Sebastodes elongatus* (Ayres) 1859
  - *Sebastodes entomelas* (Jordan and Gilbert) 1880
  - *Sebastodes helvomaculatus* (Ayres) 1859
  - *Sebastodes melanops* (Girard) 1856
  - *Sebastodes proriger* (Jordan and Gilbert) 1880
  - *Sebastodes saxicola* (Gilbert) 1890
  - *Sebastodes wilsoni* Gilbert 1915
  - *Sebastodes zacentrus* (Gilbert) 1890
- Hexagrammidae
  - *Ophiodon elongatus* Girard 1854
- Anoplopomatidae
  - *Anoplopoma fimbria* (Pallas) 1811
- Cottidae
  - *Chitonotus pugetensis* (Steindachner) 1877
  - *Hemilepidotus spinosus* (Ayres) 1855
  - *Icelinus filamentosus* Gilbert 1890
  - *Icelinus tenuis* Gilbert 1890
  - *Paricelinus hopliticus* Eigenmann and Eigenmann 1889
  - *Radulinus asprellus* Gilbert 1890
- Bothidae
  - *Citharichthys sordidus* (Girard) 1854
  - *Citharichthys stigmaeus* Jordan and Gilbert 1882
- Pleuronectidae
  - *Atheresthes stomias* (Jordan and Gilbert) 1880
  - *Embassichthys bathybius* (Gilbert) 1890
  - *Eopsetta jordani* (Lockington) 1879
  - *Glyptocephalus zachirus* Lockington 1879
  - *Isopsetta isolepis* (Lockington) 1880
  - *Lepidopsetta bilineata* (Ayres) 1855
  - *Lyopsetta exilis* (Jordan and Gilbert) 1880
  - *Microstomus pacificus* (Lockington) 1879
  - *Parophrys vetulus* Girard 1854
  - *Platichthys stellatus* (Pallas) 1811
  - *Pleuronichthys decurrens* Jordan and Gilbert 1880
- Agonidae
  - *Agonopsis emmelane* (Jordan and Starks) 1895
  - *Asterotheca infraspinata* (Gilbert) 1904
  - *Asterotheca pentacantha* (Gilbert) 1890
  - *Bathyagonus nigripinnis* Gilbert 1890
  - *Occa verrucosa* (Lockington) 1880
  - *Xeneretmus latifrons* (Gilbert) 1890
  - *Xeneretmus triacanthus* (Gilbert) 1890
- Liparidae
  - *Careproctus melanurus* Gilbert 1891
  - *Rhinoliparis attenuatus* Burke 1912

Pleuronectidae, Scorpaenidae, and Bothidae were clearly the dominant families. They comprised approximately 86% of the total number of specimens in the catch. Numerically abundant species for each of these families were:

	% of catch within family
Pleuronectidae	
Lyopsetta exilis	68
Glyptocephalus zachirus	14
Parophrys vetulus	9
Microstomus pacificus	5
Total	96
Scorpaenidae	
Sebastolobus altivelis	54
Sebastolobus alascanus	34
Total	88
Bothidae	
Citharichthys sordidus	97

Families contributing the most species were: Scorpaenidae (13 species), Pleuronectidae (11), Agonidae (7), Cottidae (6), Zoarcidae (6), and Rajidae (5).

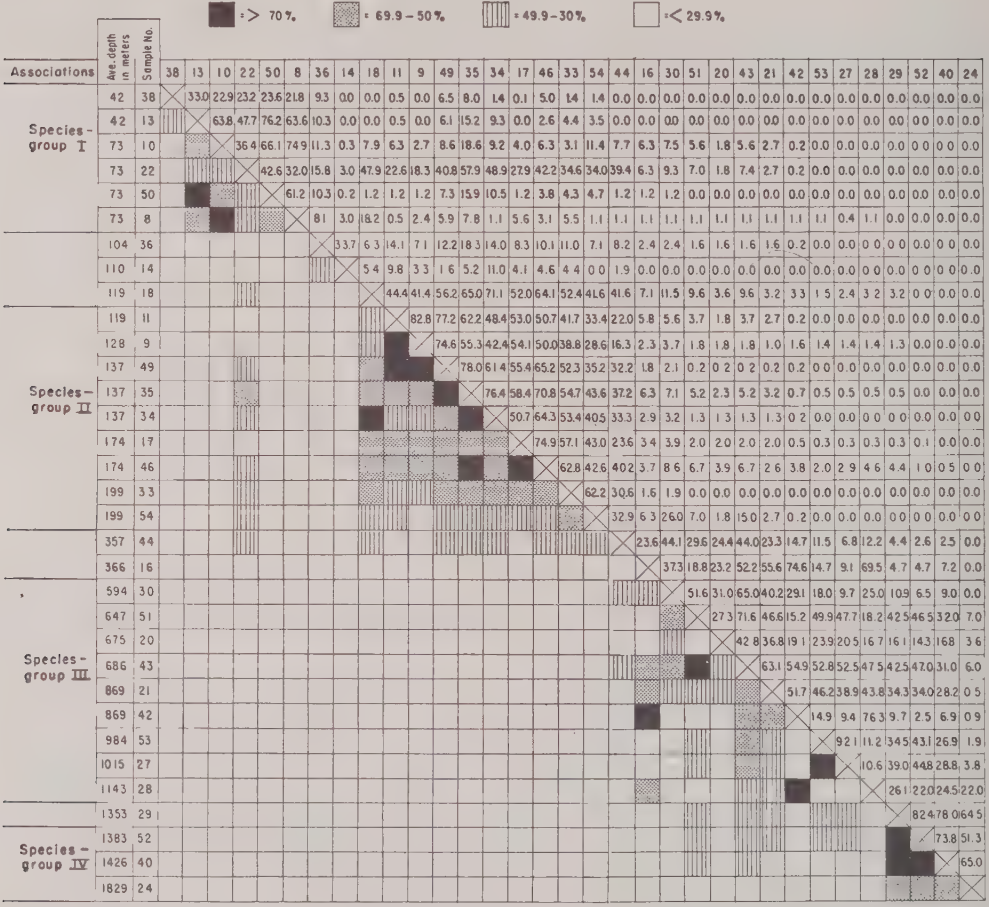
Species associations, or groups of species commonly found living together, were revealed by comparing indices of similarity among all collections (e.g., Wieser, 1960; MacFadyen, 1963). The percentage composition was computed for all species in each sample, and all possible sample pairs were compared. For each species common to both samples, the lower of the two percentage composition values was taken as a measure of species association between the two samples. The sum of these low values then provides an index of similarity for the two samples. For example, if species X, Y, and Z occurred in samples I and II at the following percentages:

	Sample I (%)	*Sample II* (%)
Species X	10	50
Species Y	75	20
Species Z	15	30

then the index of similarity is 45% for these two samples. Finally, we arranged the values obtained from all possible combinations of samples in a trellis diagram to show the relations among samples.

This trellis diagram (Fig. 2) shows the degree of similarity for samples of benthic fishes collected with increasing depth across the continental shelf and slope. Three benthic fish associations are obvious. Note the clusters of samples of high similarity (>50%) separated by regions of low similarity (<29.9%). In the region of deepest sampling a fourth association is suggested.

The dominant species, depth intervals, and average sediment types for these associations, designated as species-groups I, II, III, and IV, are given in Table II. Dominance is pronounced. Only two or three species contributed



■ :> 70%. ▒ = 69.9 – 50%. ▥ = 49.9–30%. ☐ =< 29.9%.

Associations	Ave. depth in meters	Sample No.	38	13	10	22	50	8	36	14	18	11	9	49	35	34	17	46	33	54	44	16	30	51	20	43	21	42	53	27	28	29	52	40	24
Species-group I	42	38	╳	33.0	22.9	23.2	23.6	21.8	9.3	0.0	0.0	0.5	0.0	6.5	8.0	1.4	0.1	5.0	1.4	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	42	13	▥	╳	63.8	47.7	76.2	63.6	10.3	0.0	0.0	0.5	0.0	6.1	15.2	9.3	0.0	2.6	4.4	3.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	73	10		▒	╳	36.4	66.1	74.9	11.3	0.3	7.9	6.3	2.7	8.6	18.6	9.2	4.0	6.3	3.1	11.4	7.7	6.3	7.5	5.6	1.8	5.6	2.7	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	73	22		▥	▥	╳	42.6	32.0	15.8	3.0	47.9	22.6	18.3	40.8	57.9	48.9	27.9	42.2	34.6	34.0	39.4	6.3	9.3	7.0	1.8	7.4	2.7	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	73	50		■	▒	▥	╳	61.2	10.3	0.2	1.2	1.2	1.2	7.3	15.9	10.5	1.2	3.8	4.3	4.7	1.2	1.2	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	73	8		▒	■	▥	▒	╳	81	3.0	18.2	0.5	2.4	5.9	7.8	1.1	5.6	3.1	5.5	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	0.4	1.1	0.0	0.0	0.0	0.0
	104	36							╳	33.7	6.3	14.1	7.1	12.2	18.3	14.0	8.3	10.1	11.0	7.1	8.2	2.4	2.4	1.6	1.6	1.6	1.6	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	110	14							▥	╳	5.4	9.8	3.3	1.6	5.2	11.0	4.1	4.6	4.4	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	119	18				▥					╳	44.4	41.4	56.2	65.0	71.1	52.0	64.1	52.4	41.6	41.6	7.1	11.5	9.6	3.6	9.6	3.2	3.3	1.5	2.4	3.2	3.2	0.0	0.0	0.0
Species-group II	119	11									▥	╳	82.8	77.2	62.2	48.4	53.0	50.7	41.7	33.4	22.0	5.8	5.6	3.7	1.8	3.7	2.7	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	128	9									▥	■	╳	74.6	55.3	42.4	54.1	50.0	38.8	28.6	16.3	2.3	3.7	1.8	1.8	1.8	1.0	1.6	1.4	1.4	1.4	1.3	0.0	0.0	0.0
	137	49				▥					▒	■	■	╳	78.0	61.4	55.4	65.2	52.3	35.2	32.2	1.8	2.1	0.2	0.2	0.2	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	137	35				▒					▒	▒	▒	■	╳	76.4	58.4	70.8	54.7	43.6	37.2	6.3	7.1	5.2	2.3	5.2	3.2	0.7	0.5	0.5	0.5	0.5	0.0	0.0	0.0
	137	34				▥					■	▥	▥	▒	■	╳	50.7	64.3	53.4	40.5	33.3	2.9	3.2	1.3	1.3	1.3	1.3	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	174	17									▒	▒	▒	▒	▒	▒	╳	74.9	57.1	43.0	23.6	3.4	3.9	2.0	2.0	2.0	2.0	0.5	0.3	0.3	0.3	0.3	0.1	0.0	0.0
	174	46				▥					▒	▒	▒	▒	■	▒	■	╳	62.8	42.6	40.2	3.7	8.6	6.7	3.9	6.7	2.6	3.8	2.0	2.9	4.6	4.4	1.0	0.5	0.0
	199	33				▥					▒	▥	▥	▒	▒	▒	▒	▒	╳	62.2	30.6	1.6	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	199	54				▥					▥	▥		▥	▥	▥	▥	▥	▒	╳	32.9	6.3	26.0	7.0	1.8	15.0	2.7	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Species-group III	357	44				▥					▥			▥	▥	▥		▥	▥	▥	╳	23.6	44.1	29.6	24.4	44.0	23.3	14.7	11.5	6.8	12.2	4.4	2.6	2.5	0.0
	366	16																				╳	37.3	18.8	23.2	52.2	55.6	74.6	14.7	9.1	69.5	4.7	4.7	7.2	0.0
	594	30																			▥	▥	╳	51.6	31.0	65.0	40.2	29.1	18.0	9.7	25.0	10.9	6.5	9.0	0.0
	647	51																					▒	╳	27.3	71.6	46.6	15.2	49.9	47.7	18.2	42.5	46.5	32.0	7.0
	675	20																					▥		╳	42.8	36.8	19.1	23.9	20.5	16.7	16.1	14.3	16.8	3.6
	686	43																			▥	▒	▒	■	▥	╳	63.1	54.9	52.8	52.5	47.5	42.5	47.0	31.0	6.0
	869	21																				▒	▥	▥	▥	▒	╳	51.7	46.2	38.9	43.8	34.3	34.0	28.2	0.5
	869	42																				■				▒	▒	╳	14.9	9.4	76.3	9.7	2.5	6.9	0.9
	984	53																						▥		▒	▥		╳	92.1	11.2	34.5	43.1	26.9	1.9
	1015	27																						▥		▒	▥		■	╳	10.6	39.0	44.8	28.8	3.8
	1143	28																				▒				▥	▥	■			╳	26.1	22.0	24.5	22.0
Species-group IV	1353	29																						▥		▥	▥		▥	▥		╳	82.4	78.0	64.5
	1383	52																						▥		▥	▥		▥	▥		■	╳	73.8	51.3
	1426	40																						▥		▥						■	■	╳	65.0
	1829	24																														▒	▒	▒	╳

FIG. 2. "Trellis Diagram" illustrating the degree of similarity of the benthic fish fauna at the stations on the shelf and slope off the central coast of Oregon.

from 77 to 93% (by number) of the fish fauna in each association. Also, the depth interval and sediment type associated with each species-group are different.

Although not apparent from Fig. 2, the association represented by species-group IV is distinct, based on changes in species composition. Deepwater species, *Coryphaenoides acrolepis* and *Antimora rostrata*, were dominant in these catches, whereas *Sebastolobus altivelis* and *S. alascanus* decreased relative to species-group III.

Almost one-half the total number of species of benthic fishes was found only in one association. Species limited to one association comprised 50% of the species in group I, 48% in group II, 47% in group III, and 22% in group IV. Thus the degree of fidelity, or restriction to one association, remained approximately constant with increasing depth through species-group III but decreased rapidly with group IV. This trend for deeper species to have a broader depth range is also illustrated in Fig. 3.

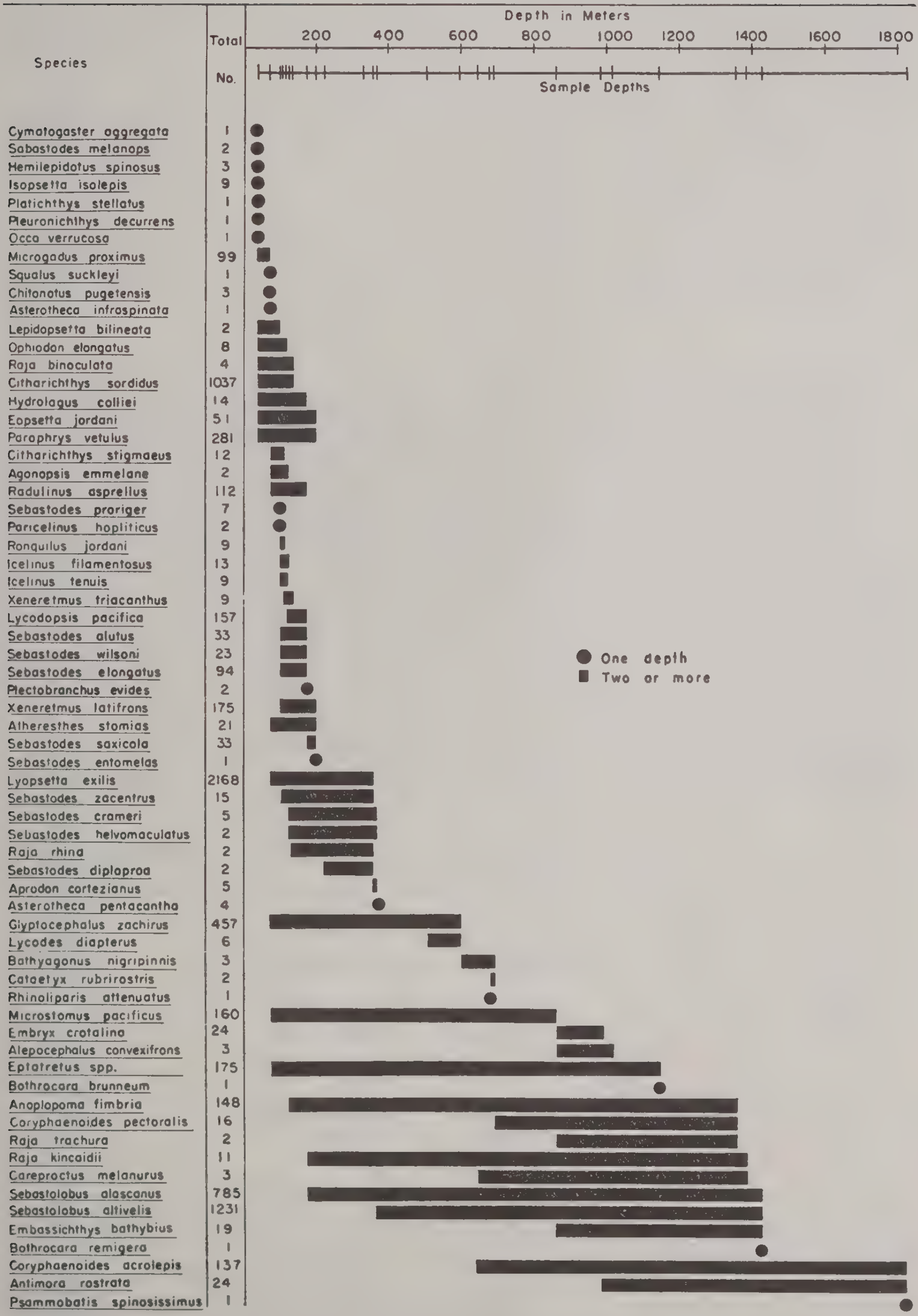


FIG. 3. Depth ranges for species of benthic fishes collected off the central coast of Oregon. (*Squalus suckleyi should be replaced with Squalus acanthias.*)

Other species were found in two or more associations, but these were usually much more abundant in one species-group than in any other, and 88% of the species exhibited high abundance (>60% of total number) in only one particular association. When species were found in more than one association, moreover, individuals of different sizes were often found in different associations. The average size of *Parophrys vetulus*, *Citharichthys sordidus*, *Eopsetta jordani*, *Microstomus pacificus*, and *Anoplopoma fimbria* increased in species-groups found in progressively deeper water. Thus overlap of the associations was small, since species generally were associated with only one species-group, or showed high abundance in one particular species-group, or were segregated by size.

ASSOCIATIONS AND SEDIMENT TYPE

The sediment texture varied from 100% sand on the upper shelf to a silty clay on the lower slope. Usually the average sediment type was different for each species association of fishes (Tables II and III), a relation previously described for benthic invertebrates (e.g. Thorson, 1955).

Sometimes species-groups and sediment types did not coincide exactly. For example, two distinct sediment types were found in the depth range of species-groups II and III, where finer sediments were collected at the deepest stations (Table III). This lack of correspondence suggests that faunal similarities are maintained in regions of sediment transition, and conversely, that factors other than sediment may govern the distribution of associations. We should be cautious in our interpretations, however. Because of the variability of sediments particularly on the upper slope and lower shelf (see Table III) the sediment sampled and the sediment trawled over could be different.

TABLE II. Depth interval, average sediment type, and dominant species for each species-group.

Species associations	Depth interval (*m*)	Avg sediment type for each species association (%)	Dominant species	% composition
I	42–73	100 sand	*Citharichthys sordidus*	64.0
			Parophrys vetulus	16.3
			Total	80.3
II	119–199	69 sand,	*Lyopsetta exilis*	66.4
		19 silt,	*Glyptocephalus zachirus*	11.4
		12 clay	Total	77.8
III	594–1143	17 sand,	*Sebastolobus altivelis*	49.7
		55 silt,	*Sebastolobus alascanus*	30.9
		28 clay	Total	80.6
IV	1383–1829	1 sand,	*Coryphaenoides acrolepis*	51.6
		53 silt,	*Sebastolobus altivelis*	26.3
		46 clay	*Antimora rostrata*	14.7
			Total	92.6

TABLE III. Sediment composition at each biological sampling location, and average sediment composition with respect to depth and the benthic fish associations.

Species-groups	Sample no.	Avg depth (*m*)	Sediment composition (%) Rock	Sand	Silt	Clay	Avg sediment composition (%)
I	38	42		100			100 sand
	13	42		100			
	10	73		100			
	22	73		100			
	50	73		100			
	8	73		100			
	36	104	100				Rock
	14	110		65	19	16	81 sand, 10 silt, 9 clay
	18	119		88	5	7	
II	11	119		89	5	6	
	9	128		73	10	17	
	49	137		89	5	6	
	35	137		89	5	6	
	34	137		89	5	6	
	17	174		56	25	19	
	46	174		87	11	2	
	33	199		23	53	24	28 sand, 48 silt, 24 clay
	54	199		23	53	24	
	12	221		47	28	25	
	31	329		53	31	16	
	44	357		23	53	24	
	16	366		52	20	28	
	26	508		38	48	14	
III	30	594		14	64	22	
	51	647		28	58	14	
	20	675		14	64	22	
	43	686		28	58	14	
	21	887		20	42	38	
	42	887		3	56	41	
	53	984		35	45	20	
	27	1,015		12	54	34	
	28	1,143		1	51	48	1 sand, 53 silt, 46 clay
	29	1,353		1	54	45	
IV	52	1,383		1	54	45	
	40	1,426		1	51	48	
	24	1,829		2	53	45	

DEPTH DISTRIBUTIONS

Figure 3 shows the depth distributions of the species collected. The depth ranges of species found on the shelf are clearly less than the ranges of species found on the slope. Some species, such as *Glyptocephalus zachirus* and *Microstomus pacificus* range from shelf waters deep into the slope waters.

Forty-two species occurred on the continental shelf; 43 occurred on the continental slope; thus, the total number of species was about the same. The total number of species collected in each association was 26 in group I, 31 in group II, 19 in group III, and only 9 in group IV.

DISCUSSION

Sampling bias is an inherent problem in any study of natural populations, such as benthic fishes. A portion of the benthic fishes along a given path will avoid or escape any net. Thus only a partial estimate of the benthic fish populations can be obtained by the use of one type of sampling equipment.

That the catch composition will be different in different types of trawls is shown by comparing our results with those obtained by Alverson et al. (1964). They used a larger net (28.7-m eastern fish trawl) and larger mesh (89–137 mm stretch) than our shrimp trawl and towed with a double rather than a single warp. As expected, the shrimp trawl retained smaller sizes of fishes than the larger fish trawl (Jurkovich, 1954; Pereyra et al., 1967). Also, the relative abundance of some species was grossly different in the two studies. Whereas Alverson et al. (1964) reported 22 species of rockfishes and 14 flatfishes off Oregon and Washington, we collected only 12 rockfishes and 13 flatfishes. *Sebastodes elongatus*, our most abundant rockfish species, was not significant in their rockfish catches off Oregon. Conversely, *Sebastodes alutus*, *Merluccius productus*, and *Squalus acanthias* were important species in their catches but were only rare or absent in our survey. Thus, the 6.7-m shrimp trawl apparently did not retain large demersal species or species which are more nektonic and may range off the bottom.

The differences between the studies may be accentuated by the fact that Alverson et al. (1964) sampled extensively off both Oregon and Washington, whereas our study was confined to a small area. By summarizing their catches over a large geographic area, they combined associations found on different sediment types, possibly explaining in part why dominant species within various depth intervals were different in the two studies.

Perhaps the combined results of both studies would provide a more accurate average picture of the benthic fish associations off Oregon. Unfortunately, there is no basis for combination; the collections were made in different areas, and Alverson et al. (1964) ranked their species by weight instead of numbers. As a result, it is not known whether the larger, more nektonic fishes, such as rockfishes and hake, are closely associated with our species-groups. Since they are more pelagic in their ecology, it may be expected that depth and sediment type are not as important to the distribution of these species as they are to the benthic species.

ACKNOWLEDGMENTS

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Morphological Variations of *Gymnodinium breve* Davis

ALEXANDER DRAGOVICH

VARIABILITY in dinoflagellates reflects internal processes and external environment and is, therefore, useful in both taxonomic and ecological studies (Bursa, 1963). Deformed Gymnodinioideae in laboratory cultures were noted by Kofoid and Swezy (1921), Lebour (1925), and Biecheler (1952). Morphological variations of dinoflagellates under natural conditions, often induced by changes in salinity and temperature or by hydrostatic pressure, occur frequently in the vicinity of estuaries (Bursa, 1963). This paper describes several variant forms of the Florida red-tide organism, *Gymnodinium breve*, observed in field samples (Fig. 1).

The fish-killing Florida red tide is a natural phenomenon in the Gulf of Mexico associated with discolored water containing dense populations of *G. breve*. *Gymnodinium breve* also occurs in Trinidad (Lackey, 1956) and is the chief suspect related to fish mortalities that occur frequently in the Orinoco River (Gulf of Paria) (Rounsefell and Nelson, 1966).

Published material on morphological variations in *G. breve* is scarce. Since 1948, when Davis described this naked dinoflagellate as a new species, few publications have been concerned with its morphology. Lackey and Hynes (1955) gave descriptions of *G. breve*; Steidinger (1964) published two photographs of *G. breve* (from living specimens); and Steidinger and Williams (1964) defined a new variation of *G. breve* and discussed cyst formation. Variation in cultured forms was reported by Wilson (1967); he also described the most common encystment stage and the general features of reproduction.

This study is based on plankton samples collected monthly from February 1964 through February 1965 at 6 locations in Tampa Bay and Charlotte Harbor (Florida), and 16 locations in neritic waters of the Gulf of Mexico (Dragovich and Kelly, 1966). The neritic stations were positioned at 5, 10, 15, and 20 miles offshore along a series of 4 transects perpendicular to the coastline. At each station the water column was sampled at 5-m intervals from surface to bottom. Station depth varied from 5-20 m.

The five morphological variations most frequently observed during this study are described in this paper, under the arbitrary des-

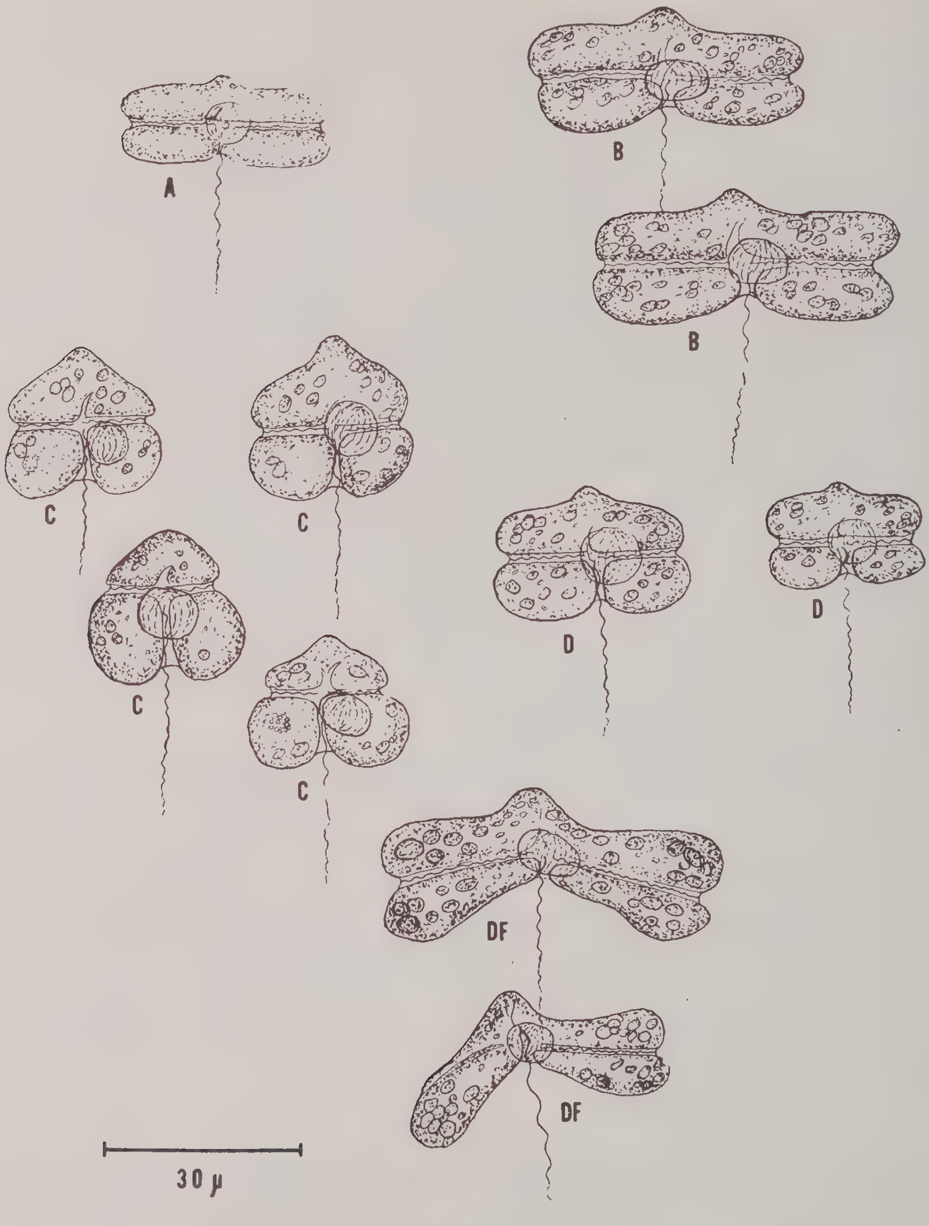

Fig. 1. Sketches of morphological variations of *Gymnodinium breve*.

ignations of forms A, B, DF, C, and D (Fig. 1). All drawings were made from living specimens.

Form A is a wide, flat cell; breadth varies from 20μ to 40μ. The cell is several times broader than long. The breadth referred to throughout this paper is the breadth across the girdle, ventral view.

Breadth is used instead of length because it is more clearly defined in *G. breve* than the length.

The cytoplasm is transparent, finely granulated, and without distinct chromatophores; in transmitted light appears pale green in color. A large nucleus is usually positioned near the center, all cells have a small apical protuberance of epicone, and a transverse groove, or girdle, is centrally located. The sulcus extends into the epicone, and both girdle and sulcus appear smooth, though slightly impressed. The organism is equipped with a transverse and a longitudinal flagellum. The transverse flagellum is within the girdle and circumscribes the cell in this form and in all other forms. No ingested food was noted.

The shape of form B is similar to that of form A but has the appearance of being slightly deformed and inflated. The breadth of the cell varies from 25μ to 60μ, and is several times greater than the length. Numerous round and discoid chromatophores are present. The clarity of the cell varies from translucent to opaque, and the appearance of the cytoplasm in transmitted light varies from light green to yellowish brown. The nucleus, epicone, sulcus, and girdle are more pronounced in form B than in form A; the flagella are the same as in A. No ingested food was observed.

Forms classified as DF are probably predivision stages of form B, but the actual division process was not observed. Form DF is generally larger than form B and measures up to 70μ wide. The cell is butterfly-shaped, and some cells have a split along the sulcus up to the epicone.

The shape of form C is suboval, and the cell breadth varies from 18μ to 40μ. The cell may contain numerous oval, suboval, and discoid chromatophores or may be without distinct chromatophores. Cell color usually is pale green or yellowish green, and the cell may be transparent, translucent, or opaque. The distinct nucleus is located centrally; in some cells, it is contained entirely in the hypocone. The epicone is smaller than the hypocone in some specimens, and the apical protuberance of the epicone was not observed in all cells. The sulcus (which extends into the epicone and at times branches) and girdle are pronounced and impressed. Cells have flagella as do forms A and B. No ingested food was noted. Form C was similar to the typical mature *G. breve* cell in cultures described by Wilson (1967).

Form D is intermediate between forms B and C, but is neither as wide as form B nor as flat as form C. The apical protuberance of the epicone and the nucleus, chromatophores, sulcus, girdle, flagellae, and color are similar to form B.

The described forms occurred at all depths; at times, all forms were present in single samples. Although similar forms were observed in earlier investigations, records of their occurrence in the field samples were made for the first time in the present study.

Form C occurred more frequently than the others and was the only one found in Charlotte Harbor (Florida). Studies have disclosed occurrences of form B during bloom and nonbloom periods of red tide. Form A occurred in the offshore waters through most of the year, but was never seen in bloom proportions. Form D was present throughout the area, but was less frequent than forms A, B, and C.

From an ecological point of view, form A may indicate unfavorable conditions for the development of red tide, and form B (and DF) favorable conditions. Forms C and D may be regarded as ecologically intermediate forms between A and B (and DF).

Culturing of these forms from single cell isolates will be required to determine whether they are the same species. Observations of unialgal cultures of *G. breve* have shown that forms B and DF may transform into type C cells (John H. Finucane, personal communication). Thus it is possible that these forms belong to the same species. Wilson (1967) reported that some of the irregularly-shaped *G. breve* cells reverted to normal cells when transferred individually with a micropipette to fresh medium.

The facts that forms observed under natural conditions and in culture differed from the original description (Davis, 1948) suggest that further and more detailed research on taxonomy and ecology of *G. breve* is needed.

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OCCURRENCE OF THE SQUID, *LOLLIGUNCULA BREVIS*, IN SOME COASTAL WATERS OF WESTERN FLORIDA

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OCCURRENCE OF THE SQUID, *LOLLIGUNCULA BREVIS*, IN SOME COASTAL WATERS OF WESTERN FLORIDA[1]

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ABSTRACT

Lolliguncula brevis (Blainville) is the dominant cephalopod in the Tampa Bay and Charlotte Harbor–Pine Island Sound areas of west Florida. Distribution and seasonal occurrence of the species are discussed. The temperature and salinity ranges at which squid occurred were 12.6 to 31.6°C and 18.19 to 36.15‰. The majority of the squid collected were immature.

This note presents information on the occurrence and distribution of squid in bays of the central west coast of Florida and adjacent neritic waters of the Gulf of Mexico. Published material pertaining to the systematics and geographical distribution of cephalopods in the Gulf of Mexico is limited to the work of Voss (1950, 1954, 1955, 1956a, 1956b). Little is known about the distribution of squid in Florida estuaries and adjoining marine waters (Tabb & Manning, 1961; Dragovich & Kelly, 1963). In Florida, squid is used extensively as bait by commercial and sport fishermen (Dragovich & Kelly, 1963), and small amounts are consumed by humans.

Samples were collected from September, 1962, through December, 1962, with a ten-foot, shrimp try-net, and from January, 1963, through December, 1964, with a 16-foot, semi-balloon trawl. Both nets had one-inch, stretch mesh. Most of the stations in Tampa Bay and the adjacent oceanic waters were sampled semimonthly during 1962, monthly during 1963, and in alternate months during 1964. Six stations in Charlotte Harbor and three in Pine Island Sound were sampled monthly only, during 1964. Water temperatures at each station were recorded with a Whitney underwater thermometer (Model T 65), or with a mercury thermometer graduated to 0.1°C. Salinity was determined by the Mohr-Knudsen method (Knudsen, 1901).

Of 648 squids collected, all except one were *Lolliguncula brevis* (Blainville), the brief squid. The single specimen was an immature *Doryteuthis*

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[1] Contribution No. 62, Tropical Atlantic Biological Laboratory, Bureau of Commercial Fisheries, Miami, Fla.

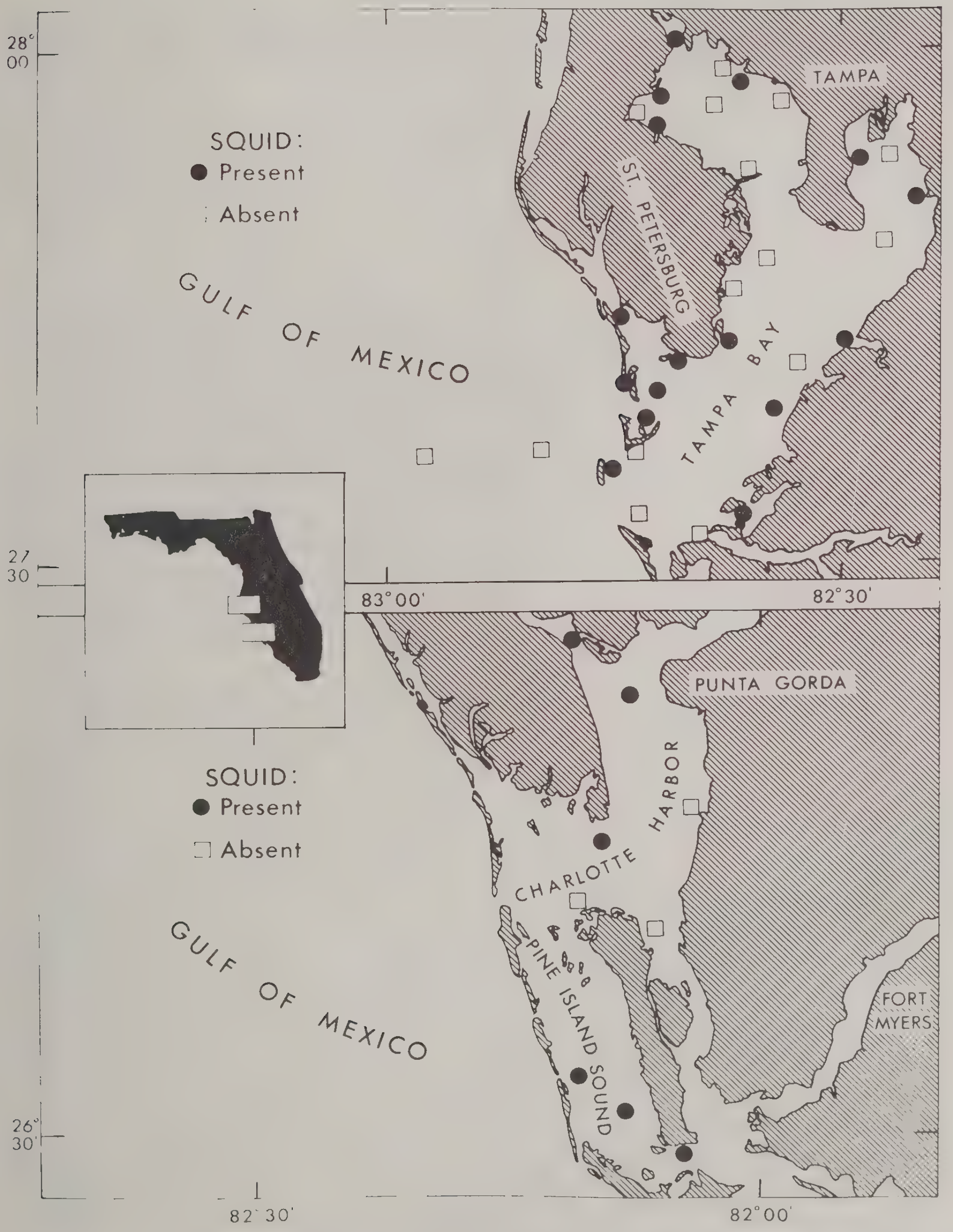
28°
00'
SQUID:
● Present
□ Absent
GULF OF MEXICO
TAMPA
ST. PETERSBURG
TAMPA BAY
27°
30'
83°00'
82°30'
PUNTA GORDA
CHARLOTTE HARBOR
SQUID:
● Present
□ Absent
GULF OF MEXICO
PINE ISLAND SOUND
FORT MYERS
26°
30'
82°30'
82°00'

FIGURE 1. Distribution of *Lolliguncula brevis* at the stations sampled in Tampa Bay, Charlotte Harbor, and Pine Island Sound, and the adjacent offshore waters of the Gulf of Mexico, September, 1962, to December, 1964.

TABLE 1

NUMBERS OF *Lolliguncula brevis* COLLECTED IN TAMPA BAY, CHARLOTTE HARBOR, AND PINE ISLAND SOUND, FLORIDA, IN DIFFERENT MONTHS

Year and location	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1963												
Tampa Bay (13 stations)	17 (8)*	14 (12)	22 (12)	8 (12)	0 (12)	27 (12)	0 (12)	0 (12)	12 (12)	13 (12)	18 (5)	0 (11)
1964												
Charlotte Harbor and Pine Island Sound (6 stations)	7 (9)	0 (4)	0 (6)	0 (6)	1 (6)	2 (6)	0 (6)	0 (6)	10 (6)	19 (6)	27 (6)	0 (6)

* The number of 10-minute trawl hauls made each month is shown in parentheses.

plei (Blainville), 116 mm long, collected in December, 1963, at the mouth of Tampa Bay; it is not included in the account that follows.

Sex and maturity were determined for all except a few immature specimens on the basis of the size-maturity relationship reported for this species by Dragovich & Kelly (1963). The dorsal mantle length (tip of the anterior lobe to the posterior end of the mantle) was measured with vernier calipers.

L. brevis is the dominant cephalopod in the Tampa Bay and Charlotte Harbor–Pine Island Sound areas. Previously, the species was reported on the west coast of Florida only from Tampa Bay (Dragovich & Kelly, 1963) and near Cape Sable, 160 miles south of Tampa Bay (Tabb & Manning, 1961). Charlotte Harbor and Pine Island Sound are two major embayments between these points. It is evident, therefore, that the species inhabits almost all the waters along the southwestern coast of Florida.

Squid were collected at 22 of the 40 stations sampled: at 16 of 29 stations in Tampa Bay (but not at 2 offshore stations), and at 6 of 9 stations in Charlotte Harbor and Pine Island Sound (Fig. 1).

Squid were collected in Tampa Bay in all months of 1963 except May, July, August, and December (Table 1); in Charlotte Harbor and Pine Island Sound, they were most abundant during September, October, and November, and were absent or scarce in the remaining months.

Both mature and immature squid were collected in each month except July (when no squid were captured). In a previous study also, mature squid were absent from the trawls during July (Dragovich & Kelly, 1963). Immature squid dominated at most of the sampling locations; 75 per cent of all squid captured were immature. Of the mature specimens, 51 per cent were male and 49 per cent female; of the immature, 89 per cent were male and 11 per cent female.

The temperature at which squid occurred ranged from 12.6 to 31.6°C, and the salinity from 18.19 to 31.15‰. This salinity range agrees with that reported by Dragovich & Kelly (1964), Gunter (1950), Tabb & Manning (1961), and Haefner (1959). *L. brevis* is one of the few cephalopods which can tolerate estuarine salinities.

The distribution of squid was not uniform (Fig. 1). In Tampa Bay, they were present in areas with soft bottoms consisting primarily of mud, clay, or silt. At most of the stations where they were absent, the bottom was covered with coarse sand and grass. At stations in Pine Island Sound and Charlotte Harbor, squid were about equally distributed over both sandy and clay (or soft) bottoms.

The survey indicated that squid inhabit shallow coastal waters of western Florida with salinities lower than those in the adjacent waters of the Gulf of Mexico. On the basis of this and previous studies (Tabb & Manning, 1961; Dragovich & Kelly, 1963), *L. brevis* may be considered a euryhaline species and an important component of the resident, estuarine biota of western Florida.

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SUMARIO

PRESENCIA DEL CALAMAR *Lolliguncula brevis* EN ALGUNAS AGUAS COSTERAS DE LA REGION OCCIDENTAL DE LA FLORIDA

Lolliguncula brevis (Blainville) es el cefalópodo predominante en Tampa Bay y Charlotte Harbor. Se discuten la distribución y ocurrencia estacional de la especie. Los valores de la temperatura y la salinidad de los lugares donde se encontró el calamar fueron de 12.6 a 31.6°C y de 18.19 a 36.15‰, respectivamente. La mayoría de los ejemplares colectados no estaban sexualmente maduros. La especie se encuentra en casi todas las aguas a lo largo de la costa sudoeste de la Florida. Basándose en ésto y en estudios previos, *L. brevis* puede ser considerada una especie eurihalina y un componente importante de la biota estuarina del oeste de la Florida.

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Growth Changes of the Bloater (*Coregonus hoyi*) of the Apostle Islands Region of Lake Superior

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Growth Changes of the Bloater (*Coregonus hoyi*) of the Apostle Islands Region of Lake Superior[1]

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ABSTRACT

Studies were based primarily on 3,097 bloaters collected in experimental gill nets and bottom trawls fished in 1958–65 in the Apostle Islands region of Lake Superior.

The average size of bloaters increased considerably during the period. The percentage longer than 8.9 inches increased from 45% in 1959 to 99% in 1965. Calculated lengths were without exception higher in 1962–65 than in 1958–61. Growth in length and weight showed nearly steady improvement from 1951 to 1964. The species composition of chubs has apparently changed considerably over the past 40 years. The bloater has replaced the shortjaw cisco (*C. zenithicus*) as the principal species in commercial landings of chubs in Wisconsin.

Annulus formation of bloaters extended from mid-May to August. Growth was slow during the spring and early summer but increased sharply in August. Age-group VI was dominant in the samples. Fluctuations in year-class strength were slight.

Females outnumbered males in all age groups above III. The sex composition varied according to season of capture. Some bloaters matured at age II and all fish older than III were mature. The shortest length of mature bloaters was 6.0 inches for males and 7.0 inches for females; all fish longer than 8.4 inches were mature. Apostle Island bloaters spawn principally in February and March. The average number of eggs produced by 20 females, 8.4 to 11.7 inches long, was 6,533. Crustaceans were the most common food.

INTRODUCTION

The bloater (*Coregonus hoyi*) is the most common of five species of chubs in Lake Superior. The other species are the blackfin cisco (*C. nigripinnis*), shortjaw cisco (*C. zenithicus*), shortnose cisco (*C. reighardi*), and kiyi (*C. kiyi*). The chubs are the deepwater members of an extremely complex subgenus (*Leucichthys*). Because they vary widely in size, shape, and systematic characters, correct species identification is often difficult, and sometimes impossible among the smaller individuals. The bloater, however, is relatively easy to identify in Lake Superior because of its protruding mandible (usually with a pronounced symphyseal knob), relatively small eye, long paired fins, and rather heavily pigmented mouth parts.

The bloater is most abundant in Lake Superior at depths of 30 to 60 fathoms, but some have been taken as shallow as 10 and as deep as 89 fathoms (Dryer, 1966). The name "bloater" originates from the bloated appearance of the fish after it is brought to the surface from deep water. The bloated condition disappears when the gas is released from the swim bladder. Fishermen of the Great Lakes broadly apply the term "bloater" to all small chubs, most of which are *C. hoyi*, the smallest and slowest growing chub.

Chubs have become increasingly important in the Lake Superior catch since the progressive decline of the lake trout (*Salvelinus namaycush*) began in the early 1950's and the subsequent closure of the commercial lake trout fishery in 1962. The contribution of chubs to the total U. S. catch rose from 0.2% (29,000 pounds) in 1950 to 13% (1.6 million pounds) in 1963. They contributed 21% of the total value of the catch in 1963. Wisconsin has dominated in the production of chubs in most of the years for which statistics are available (Baldwin and Saalfeld, 1962).

The bloater probably did not gain commercial importance in Lake Superior until recently. In the 1930's the shortjaw cisco predominated in the chub fishery (Van Oosten, 1937), but in 1965 bloaters composed about 90% of the commercial landings of chubs at Bayfield, Wisconsin.

Most published studies of bloaters were conducted on Lake Michigan. Koelz (1929) made observations on bloaters in all the Great Lakes and Pritchard (1931) studied the age, growth, and food of bloaters in Lake Ontario.

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[1] Contribution No. 367 of the Ann Arbor Biological Laboratory, U. S. Bureau of Commercial Fisheries.

TABLE 1.—*Number of bloaters used in the study of age and growth in the Apostle Islands region of Lake Superior, 1958–65. [Dashes indicate meshes not fished]*

Date	Mesh size (inches, stretched measure)												Total
	1	1½	2	2¼	2⅜	2½	2¾	3	3½	4	4½	5	
1958													
19 Sept.	–	–	–	–	33	25	–	–	–	–	–	–	58
22 Oct.	31	46	64	15	–	–	–	–	–	–	–	–	156
1959													
3 June	35	26	–	–	–	15	–	11	7	2	1	1	98
1960													
28 April	–	124	–	–	–	–	–	–	–	–	–	–	124
1961													
18 May	–	10	86	–	–	–	–	–	–	–	–	–	96
1962													
2 Oct.	5	13	70	–	–	22	–	2	4	2	1	1	120
1963													
26 March	–	10	71	–	–	6	–	–	–	–	–	–	87
1964													
26 Aug.	–	27	66	37	–	35	–	–	–	–	–	–	165
1965													
22 May	–	–	71	63	–	27	5	8	–	–	–	–	174
Total	71	256	428	115	33	130	5	21	11	4	2	2	1,078

TABLE 2.—*Length distribution of bloaters captured in experimental gill nets, 1958–65. [Asterisks indicate modes]*

Total length (inches)	Year of capture							
	1958	1959	1960	1961	1962	1963	1964	1965
5.0– 5.4	–	–	–	–	2	–	–	–
5.5– 5.9	–	–	2	–	–	–	–	–
6.0– 6.4	–	–	5	–	3	–	–	–
6.5– 6.9	–	5	9	2	–	–	–	–
7.0– 7.4	3	–	7	1	–	–	–	–
7.5– 7.9	10	3	1	3	–	–	–	–
8.0– 8.4	20	9	4	13	1	–	1	–
8.5– 8.9	*76	*37	17	25	4	8	2	2
9.0– 9.4	64	29	*52	*34	18	23	18	16
9.5– 9.9	35	8	20	16	30	*32	58	75
10.0–10.4	5	4	7	1	*36	19	*60	*128
10.5–10.9	–	3	–	1	18	4	22	82
11.0–11.4	1	–	–	–	3	–	4	21
11.5–11.9	–	–	–	–	4	–	–	3
12.0–12.4	–	–	–	–	1	1	–	2
Number of fish	214	98	124	96	120	87	165	329
Average fish length	9.0	8.9	8.8	9.0	9.9	9.7	10.0	10.3
Percentage over 8.9 inches	49.1	44.9	63.7	54.2	91.7	90.8	98.2	99.4

For Lake Michigan, Jobes (1949a) reported on the age, growth, and bathymetric distribution; Moffett (1957) and Smith (1964) described changes in the abundance and average size; Bersamin (1958) and Wells and Beeton (1963) reported on the food; and Wells (1966) studied the seasonal and depth distribution of the larvae.

MATERIALS AND METHODS

This study was based primarily on 3,097 bloaters collected in experimental gill nets and trawls fished by the Bureau's R/V *Siscowet* in 1958–65 in the Apostle Islands region of western Lake Superior. Analysis of age and growth was based on 1,078 fish captured in experimental gill nets with stretched mesh sizes of 1 to 5 inches (Table 1). All collections were complete catches or random samples.

The number of fish used in the different phases of this study varied by the amount of appropriate data available or the number of fish required for various analyses. The numbers and sources of materials used for each phase are given in the text. Field techniques for collecting data from fish and analyses used for this report were similar to those described by Dryer and Beil (1964).

The possibility of bias through gear selection was recognized because the samples were collected from gill nets of different mesh sizes in different years. In general, more bloaters were taken in the larger meshes during the later years of collection (Table 1). Since larger meshes could be expected to capture larger fish, estimates of age composition, year-class strength, size at capture, growth, and sex composition could be prejudiced by differences in mesh sizes of the sampling gear.

The extent to which differences in mesh sizes affected the data was investigated by comparing data from fish taken in a variety of meshes with those from identical meshes for each year of collection. The trends described in this paper were the same for both series; the changes in average size and growth clearly were real and not a reflection of differences in gear. The age and year-class composition of the samples were nearly identical and year-to-year changes in average size and rate of growth were parallel for both sets of data.

Because bias through gear selection appeared to be minimal, I believe that all the fish in the annual samples from various mesh sizes offer a more valid description of the population.

The length–weight relation of bloaters from the Apostle Islands region had the equation: $\text{Log } W = -2.45097 + 3.104 \log L$, where W = weight in ounces, and L = total length in inches.

TABLE 3.—*Length distribution and average weights of different age groups of bloaters taken in 1958–61 and 1962–65*

Total length (inches)	Age group and year of collection																	
	I		II	III		IV		V		VI		VII		VIII		IX		X
	1958–1961	1962–1965	1958–1961	1958–1961	1962–1965	1958–1961	1962–1965	1958–1961	1962–1965	1958–1961	1962–1965	1958–1961	1962–1965	1958–1961	1962–1965	1958–1961	1962–1965	1962–1965
5.0– 5.4	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
5.5– 5.9	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
6.0– 6.4	–	3	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
6.5– 6.9	–	–	13	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–
7.0– 7.4	–	–	10	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
7.5– 7.9	–	–	2	4	–	4	–	5	–	1	–	1	–	–	–	–	–	–
8.0– 8.4	–	–	1	15	1	10	1	10	–	8	–	2	–	1	–	–	–	–
8.5– 8.9	–	–	3	12	–	17	3	46	3	40	5	26	3	7	2	1	–	–
9.0– 9.4	–	–	–	–	6	24	9	48	12	54	18	31	11	19	7	2	3	–
9.5– 9.9	–	–	–	–	8	9	27	12	36	27	35	26	27	5	19	3	9	1
10.0–10.4	–	–	–	–	1	–	23	3	37	3	58	5	36	4	21	2	5	1
10.5–10.9	–	–	–	–	–	–	3	–	20	1	26	–	21	1	9	2	1	3
11.0–11.4	–	–	–	–	–	–	2	–	2	–	9	–	3	–	3	1	1	–
11.5–11.9	–	–	–	–	–	–	–	–	1	–	1	–	2	–	1	–	2	–
12.0–12.4	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	–	–	1
Total	1	5	35	34	16	64	69	124	111	135	153	91	103	37	62	11	21	6
Average length	5.8	5.9	7.1	8.2	9.5	8.9	9.9	9.0	10.1	9.2	10.1	9.3	10.1	9.3	10.1	10.0	10.1	10.8
Average weight (ounces)	1.0	1.0	1.6	2.6	3.8	3.2	4.4	3.3	4.6	3.5	4.7	3.6	4.7	3.7	4.6	4.4	4.7	5.9

The body-scale relation for Apostle Islands bloaters was based on the average diameters of three scales from each of 776 fish. A plot of average scale diameters and fish lengths by 0.5-inch intervals indicated that the relation was linear. The fitted straight line had the equation: $L = 0.848 + 0.0488\ S$, where L = total length of fish in inches, and S = scale diameter ($\times$ 43) in millimeters.

Calculations of length were made with a nomograph based on the fitted line.

The sexes were combined for all computations of average size and growth because sex differences were negligible and without trend.

CHANGES IN SIZE AND RATE OF GROWTH

Average Size

The average size of bloaters in the Apostle Islands region has increased considerably in recent years. The length composition of bloaters from experimental gill nets changed little in 1958–61 but in 1962 the average lengths of the fish began to increase (Table 2). Mean lengths increased from 8.9 inches in 1958–61 to 10.0 inches in 1962–65. The modal lengths increased from 8.5–8.9 inches in 1958–59 to 10.0–10.4 inches in 1962 and 1964–65. The percentage of bloaters longer than 8.9 inches increased from 44.9% in 1959 to 99.4% in 1965.

TABLE 4.—*Length distribution of bloaters taken in 1½- and 2-inch-mesh gill nets, 1958–65*[1]

Total length (inches)	1½-inch mesh							2-inch mesh						
	1958	1959	1960	1962	1963	1964	1965	1958	1959	1960	1962	1963	1964	1965
5.5– 5.9	–	–	2	–	–	–	–	–	–	–	–	–	–	–
6.0– 6.4	–	–	5	–	–	–	–	–	–	–	–	–	–	–
6.5– 6.9	1	–	9	–	–	–	–	–	–	–	–	–	–	–
7.0– 7.4	1	–	7	–	–	–	1	–	–	–	–	–	–	–
7.5– 7.9	8	2	1	–	–	1	7	–	–	1	–	–	–	–
8.0– 8.4	28	7	4	1	–	2	9	3	1	3	–	–	–	–
8.5– 8.9	7	20	17	2	2	5	22	21	7	23	1	8	–	1
9.0– 9.4	3	18	52	4	6	21	31	34	18	60	11	17	9	13
9.5– 9.9	–	3	20	1	7	32	38	16	17	29	26	29	26	48
10.0–10.4	–	–	7	5	2	9	32	–	14	9	26	20	24	55
10.5–10.9	–	–	–	1	1	–	11	–	–	–	5	3	5	22
11.0–11.4	–	–	–	–	–	–	1	–	–	–	1	–	–	6
11.5–11.9	–	–	–	–	–	–	–	–	–	–	2	–	–	–
Number of fish	48	50	124	14	18	70	152	74	57	125	72	77	64	145
Average length	8.3	8.9	8.8	9.6	9.6	9.5	9.5	9.2	9.6	9.3	10.0	9.7	9.9	10.1

[1] Includes all bloaters captured in the two mesh sizes; fish were not separated by mesh size in 1961.

TABLE 5.—*Calculated total length (inches) of bloaters, 1958–61 and 1962–65*

Age group and date	Number of fish	Calculated length at end of year of life									
		1	2	3	4	5	6	7	8	9	10
I											
1958–61	1	5.7	–	–	–	–	–	–	–	–	–
1962–65	5	4.0	–	–	–	–	–	–	–	–	–
II											
1958–61	35	4.0	6.7	–	–	–	–	–	–	–	–
III											
1958–61	34	4.3	6.7	7.9	–	–	–	–	–	–	–
1962–65	16	3.9	6.9	8.7	–	–	–	–	–	–	–
IV											
1958–61	64	4.2	6.0	7.6	8.7	–	–	–	–	–	–
1962–65	69	4.0	6.7	8.3	9.4	–	–	–	–	–	–
V											
1958–61	124	3.8	5.7	6.9	7.9	8.6	–	–	–	–	–
1962–65	111	4.0	6.3	7.9	9.0	9.7	–	–	–	–	–
VI											
1958–61	135	3.6	5.3	6.4	7.4	8.3	8.9	–	–	–	–
1962–65	153	4.0	6.0	7.3	8.4	9.2	9.9	–	–	–	–
VII											
1958–61	91	3.6	5.1	6.1	7.1	7.9	8.5	9.1	–	–	–
1962–65	103	3.7	5.4	6.6	7.6	8.5	9.4	9.9	–	–	–
VIII											
1958–61	37	3.4	4.8	5.8	6.7	7.4	8.2	8.7	9.2	–	–
1962–65	62	3.7	5.0	6.1	7.0	7.8	8.6	9.3	9.9	–	–
IX											
1958–61	11	3.3	5.0	6.0	6.8	7.5	8.2	8.8	9.5	9.9	–
1962–65	21	3.5	4.9	5.8	6.7	7.4	8.1	8.8	9.4	9.9	–
X											
1962–65	6	3.5	4.8	5.7	6.5	7.3	8.0	8.7	9.3	10.1	10.6
Grand average[1]											
1958–61		3.8	5.6	6.7	7.6	8.2	8.6	9.2	9.7	10.1	–
1962–65		3.9	5.9	7.2	8.2	8.9	9.4	10.0	10.6	11.2	11.7

[1] Based on the successive addition of mean increments beyond the 6th year of life.

The increase in size in recent years is further illustrated by the length distributions and average weights of the different age groups in 1958–61 and 1962–65 (Table 3). The average size of the few I-group fish was nearly identical for the two periods but at ages III–VII, bloaters in 1962–65 were 0.8 to 1.3 inches longer and 1.1 to 1.3 ounces heavier than those taken in 1958–61.

Because the average size of the bloaters was affected to some extent by the mesh size of the gill nets from which they were taken, inquiry was made into annual changes in average size of fish taken from identical meshes in different years of collection (Table 4).

The average size of the bloaters from identical meshes also increased during 1958–65. The mean lengths of all bloaters captured in 1½-inch-mesh gill nets increased from 8.3 inches in 1958 to 9.6 inches in 1962–63 and 9.5 inches in 1964–65. The average lengths of fish from 2-inch-mesh nets increased from 9.2 inches in 1958 to 10.1 inches in 1965.

Records from earlier studies give evidence that an increase in the size of bloaters in Lake Superior may have taken place over the past 40 years. Of 199 bloaters examined from 2½- and 4½-inch-mesh gill nets fished in the Apostle Islands region in 1922, only two were longer than 9.5 inches (Koelz, 1929). Data collected in the Apostle Islands region by the Bureau's R/V *Cisco* in 1953 show that bloaters from 1½-inch-mesh nets averaged 8.1 inches, compared with 8.3 inches in 1958 and 9.6 inches in 1962–63 for the present study. Bloaters from 2-inch-mesh nets averaged 8.8 inches in 1953, compared with 9.2 inches in 1958 and 10.1 inches in 1965.

Since the increase in average size was real, the data from all meshes were used for the study of growth, regardless of slight differences in the average mesh sizes from which the fish were removed.

Growth in Length

The increase in average size of bloaters from the Apostle Islands region was accompanied by a marked improvement in growth in recent

TABLE 6.—*Calculated weight (ounces) of bloaters, 1958–61 and 1962–65. [Weights were computed from the calculated lengths of Table 5 by means of the general length-weight relation. Increments are in parentheses]*

Years of capture	Computed weight at end of year of life									
	1	2	3	4	5	6	7	9	9	10
1958–61	0.22 (0.22)	0.74 (0.52)	1.30 (0.56)	1.92 (0.62)	2.43 (0.51)	2.82 (0.39)	3.47 (0.65)	4.09 (0.62)	4.64 (0.55)	–
1962–65	0.24 (0.24)	0.87 (0.63)	1.62 (0.75)	2.43 (0.81)	3.13 (0.70)	3.71 (0.58)	4.50 (0.79)	5.39 (0.89)	6.39 (1.00)	7.32 (0.93)

years. With few exceptions, the calculated lengths of the age groups were higher in 1962–65 than in 1958–61 (Table 5). The 5th year calculated length of the V group, for example, was 1.1 inches longer in 1962–65 than in 1958–61. The grand average calculated lengths of bloaters were longer without exception in 1962–65 than in 1958–61. Fish in 1958–61 grew 3.8 inches by the end of the 1st year but did not reach 10.0 inches until the 9th year of life. Bloaters taken in 1962–65 were only slightly longer at the end of the 1st year (3.9 inches) but reached 10.0 inches at the end of the 7th year, 2 years earlier than fish taken in 1958–61.

The systematic decline in calculated growth rate with increase in age, observed repeatedly among many other species, held true for Apostle Islands bloaters (Table 5). Voluminous reviews have been published on discrepancies of this type and most investigators agree that the decline in calculated lengths can be traced to two major sources of bias: gear selection of the larger fish in the younger age groups and the progressive selection of the faster growing fish by the fishery. The selective action of the gear is most pronounced on fish captured in gill nets of a single mesh size. Only fish of a definite size range are vulnerable to a specific mesh size, leaving free those individuals which are either too large or small to become entangled in the net. Gill nets of graded mesh sizes, such as the experimental gill nets used in this study, greatly reduce bias through gear selection because fish of a much greater range in size are vulnerable to the gear. Gear selection in the present study, therefore, may not be important in the cause of systematic discrepancies in calculated lengths of Apostle Islands bloaters. Also, the fishery for bloaters in the Apostle Islands region probably is not intensive enough to remove significant numbers of the faster growing fish.

The systematic decline in calculated lengths of bloaters in this study may reflect in part the improved growth in recent years.

Growth in Weight

Growth in weight of Apostle Islands bloaters, like growth in length, was faster in 1962–65 than in 1958–61 (Table 6). Fish taken in the later period were 0.02 ounces heavier at the end of the 1st year of life and 1.75 ounces heavier at the end of the 9th year. The largest annual increment in weight was 1.0 ounce in the 9th year (1962–65 samples). Bloaters weighed only 7.3 ounces at the end of 10 years of life.

Annual Changes in Growth

Growth in length and weight of Apostle Islands bloaters showed nearly steady improvement from 1951 to 1964. By the method described in detail by Hile (1941), the best represented age groups (IV–VIII) were subjected to a quantitative analysis by which the percentage deviations in growth were calculated from the 14-year (1951–64) mean.

The percentage deviations for growth in length were negative in 1951–58 (range, –13.9 to –0.9%) and above average in 1959–64 (range, 1.9 to 18.5%). Improvement was especially marked in 1958–61 when the percentage deviations increased from –4.7 to 14.6% (Figure 1).

With only two exceptions (those of 1958 and 1962), growth in weight improved in each successive year from 1951 to 1964 (Figure 1). The deviations increased over the 14-year period from –49.4% in 1951 to 47.4% in 1964.

Growth of lake herring (*C. artedi*) from the Apostle Islands also has improved in recent years (Dryer and Beil, 1964). The percentage deviations in growth in length increased from –23.5% in 1946 to 16.3% in 1959.

No explanation can be offered for the improved growth of bloaters in recent years. Such factors as meteorological conditions, fluctuations in lake levels, changes in basic productivity and chemical characteristics of the lake, and changes in fish populations have been considered, but no evidence has been found that any one of these factors is responsible for the striking improvement in growth of bloaters.

The only known major changes that have taken place in Lake Superior are in fish populations. The sea lamprey (*Petromyzon marinus*) became established in the late 1940's and the abundance of lake trout declined drastically by the late 1950's. Bloaters, which were a primary food of lake trout (Dryer, Erkkila, and Tetzloff, 1965) were relieved of much predation and may have increased in abundance as they did in Lake Michigan under similar conditions (Moffett, 1957; Smith, 1964). Predation on bloaters may also have been reduced by the presence of smelt (*Osmerus mordax*) which became an important food of lake trout. An increase in abundance would not, however, be expected to favor improved growth.

The stocks of lake herring observed in Lake Superior are also undergoing changes. Abundance of lake herring began to decrease in the mid-1950's and their size and growth rate improved. The unknown conditions that are favoring improved growth for bloaters appear also to favor the lake herring, and seem not to be related to increase or decrease in abundance.

CHANGES IN SPECIES COMPOSITION AND ABUNDANCE OF CHUBS

Estimates of changes in species composition and abundance of chubs based on gill net catches were made difficult by the increased average size and rate of growth of bloaters in recent years. As the average size of bloaters increased, they became more vulnerable to commercial chub nets (minimum legal mesh size is 2⅜ inches in Wisconsin and 2½ inches in Michigan) and consequently were far more abundant in the catches than in former years.

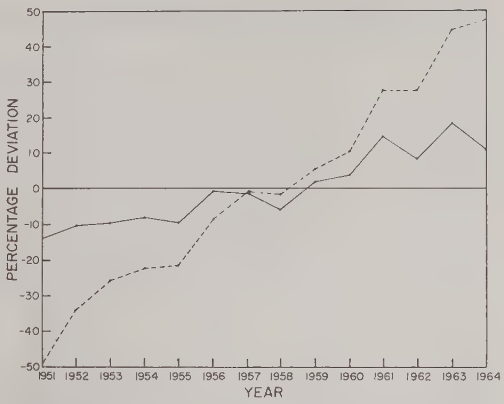

FIGURE 1.—Annual changes in growth in length (solid line) and weight (broken line) of bloaters in the Apostle Islands region.

The records of Koelz (1929) for Lake Superior indicated that bloaters were common in 1½-inch-mesh gill nets fished in Whitefish Bay and at Marquette in 1921–22, but were taken only occasionally in mesh sizes of 2½, 2⅝, and 2¾ inches fished in other areas of the lake. (He listed the bloater as common in a 4½-inch-mesh gill net lifted north of the Apostle Islands in 1922.) The largest bloater taken by Koelz in Lake Superior was 11.9 inches, and nearly all of his fish were shorter than 9.5 inches. Mesh sizes of 2½ to 2¾ inches from which most of Koelz' samples were taken would not be expected to capture sizable numbers of bloaters if most of the fish were shorter than 9.5 inches.

Despite the obvious bias from increased vulnerability of bloaters to the fishing gear in recent years, the immense changes in gill net catches over the past 40 years strongly suggest that real changes have actually occurred in the species composition of chubs and abundance of bloaters.

Koelz (1929) observed a lift of chub nets from the Apostle Islands region in 1922, and reported that the catch from 2½- to 2¾-inch-mesh gill nets set in 15–20 fathoms included 300 shortjaw ciscoes but only one each of bloater, blackfin cisco, and shortnose cisco. Van Oosten (1937) stated that in the mid-

TABLE 7.—*Percentage of bloaters with completed annuli on various dates, 1965.* [*Number of fish in parentheses*]

Date	Percentage with completed annuli in age group								Ages combined
	III	IV	V	VI	VII	VIII	IX	X	
20 May	100 (1)	25 (4)	11 (35)	0 (57)	7 (43)	0 (26)	0 (5)	0 (3)	5 (174)
15 June	100 (2)	42 (19)	23 (52)	14 (37)	17 (29)	0 (8)	– –	– –	22 (147)
24 July	100 (3)	77 (17)	49 (39)	28 (39)	55 (31)	16 (19)	0 (1)	– –	44 (149)
31 August	100 (3)	100 (47)	100 (47)	100 (31)	100 (27)	100 (6)	– –	– –	100 (161)

1930's the shortjaw cisco was the only large chub common enough to support a commercial fishery in Lake Superior. He indicated that the shortjaw cisco ranked second in abundance only to the lake herring.

In contrast to earlier catches, bloaters were overwhelmingly dominant in catches of recent years. The bloater composed over 90% of the total catch of chubs by the *Siscowet* from the Apostle Islands region in 1958–65. Gill nets of the same mesh sizes fished in the same area where Koelz observed the lift of chub nets in 1922 yielded 92% bloaters and 8% shortjaw ciscoes. Examination of 681 chubs from com-

TABLE 8.—*Calculated growth in total length (inches) and percentage of the season's growth completed by bloaters of different age groups on various dates, 1965*

Age group and item	Date of collection					Full-season growth in 1965[1]
	20 May	15 June	24 July	31 August	27 Sept.	
III						
Current-season growth	0.30	0.43	0.40	0.68	1.00	1.05
Percentage completed	28.6	41.0	38.1	64.8	95.2	100.0
Number of fish	1	2	3	3	8	22
IV						
Current-season growth	0.02	0.14	0.29	0.50	0.60	0.65
Percentage completed	3.1	21.5	44.6	76.9	92.3	100.0
Number of fish	4	19	17	47	17	61
V						
Current-season growth	0.02	0.07	0.18	0.49	0.67	0.59
Percentage completed	3.4	11.9	30.5	83.1	113.6	100.0
Number of fish	35	52	39	47	19	39
VI						
Current-season growth	0.00	0.03	0.07	0.40	0.54	0.53
Percentage completed	0.0	5.7	13.2	75.5	101.9	100.0
Number of fish	57	37	39	31	18	15
VII						
Current-season growth	0.01	0.04	0.14	0.39	0.43	0.44
Percentage completed	2.3	9.1	31.8	88.6	97.7	100.0
Number of fish	43	29	31	27	14	12
VIII						
Current-season growth	0.00	0.00	0.04	0.32	0.35	0.38[2]
Percentage completed	0.0	0.0	10.5	84.2	92.1	100.0
Number of fish	26	8	19	6	2	2
IX						
Current-season growth	0.00	–	0.00	–	–	0.23
Percentage completed	0.0	–	0.0	–	–	100.0
Number of fish	5	–	1	–	–	2
X						
Current-season growth	0.00	–	–	–	–	–
Percentage completed	0.0	–	–	–	–	–
Number of fish	3	–	–	–	–	–
Average percentage[3]	1.5	10.8	25.2	80.4	101.0	100.0
Percentage of full-season growth completed						
In month	5	11	14	50	20	–
By end of month	5	16	30	80	100	–

[1] Based on samples collected on 16 November 1965.

[2] Determined by calculation from scale measurements from the next higher age group in the same collection.

[3] Weighted means.

TABLE 9.—*Age and year-class composition of bloaters, 1958–65.* [*Asterisks indicate dominant year classes*]

Item	I	II	III	IV	V	VI	VII	VIII	IX	X
1958										
Year class	–	1956	1955	1954	*1953	1952	1951	1950	1949	–
Number	–	7	18	28	72	56	26	4	3	–
Percentage	–	3.3	8.4	13.1	33.6	26.2	12.1	1.9	1.4	–
1959										
Year class	–	1957	1956	1955	1954	*1953	1952	1951	1950	–
Number	–	3	6	14	11	24	20	16	4	–
Percentage	–	3.1	6.1	14.3	11.2	24.5	20.4	16.3	4.1	–
1960										
Year class	1959	1958	1957	1956	1955	*1954	*1953	1952	1951	–
Number	1	23	1	11	21	27	27	11	2	–
Percentage	0.8	18.5	0.8	8.9	16.9	21.8	21.8	8.9	1.6	–
1961										
Year class	–	1959	1958	1957	1956	*1955	1954	1953	1952	–
Number	–	2	9	11	20	28	18	6	2	–
Percentage	–	2.1	9.4	11.5	20.8	29.2	18.7	6.2	2.1	–
1962										
Year class	1961	–	1959	1958	*1957	1956	1955	1954	1953	1952
Number	5	–	8	18	28	26	15	13	5	2
Percentage	4.2	–	6.7	15.0	23.2	21.7	12.5	10.8	4.2	1.7
1963										
Year class	–	–	–	1959	1958	*1957	1956	1955	1954	–
Number	–	–	–	7	11	29	25	9	6	–
Percentage	–	–	–	8.0	12.6	33.5	28.7	10.3	6.9	–
1964										
Year class	–	–	1961	1960	1959	*1958	1957	1956	1955	1954
Number	–	–	7	40	37	41	20	14	5	1
Percentage	–	–	4.2	24.2	22.5	24.9	12.1	8.5	3.0	0.6
1965										
Year class	–	–	1962	1961	1960	*1959	1958	1957	1956	1955
Number	–	–	1	4	35	57	43	26	5	3
Percentage	–	–	0.6	2.3	20.1	32.8	24.7	14.9	2.9	1.7
Average percentage	0.6	3.4	4.5	12.2	20.1	26.8	18.9	9.7	3.3	0.5

mercial landings at Bayfield in 1965 revealed that bloaters composed 90% of the catch; shortjaw cisco, 8%; and kiyi, 2%.

Moffett (1957) and Smith (1964) also noted major changes in the species composition of chubs in Lake Michigan. The abundance of bloaters increased greatly between 1932 and 1961 and the large deepwater cisco (*C. johannae*) and blackfin cisco declined to extinction. The change in species composition was attributed to the combined effects of the predatory sea lamprey and the commercial fishery. The bloater, relieved of predation by the lake trout and burbot (*Lota lota*), became increasingly abundant in Lake Michigan and ultimately represented over 99% of the chubs. The larger chubs became nearly extinct in the early 1960's (Wells, 1966).

BIOLOGICAL CHARACTERISTICS

Long-term observations of the biological characteristics of the bloater may be helpful in explaining the probable increased abundance, larger average size, and improved growth in recent years. Although a longer series of data than now available will be required, the following observations may provide a base for future comparisons.

Annulus Formation and Progress of the Season's Growth

The period of annulus formation for bloaters from the Apostle Islands in 1965 extended from mid-May to August (Table 7). Although the earliest collection of 20 May included several fish (5%) which had begun new growth, only 44% of the fish captured on 24 July had formed an annulus. All of the bloaters taken on 31 August had new growth. The younger bloaters, in common with most species of fish, began new growth earlier than the older ones. With few exceptions, the percentage of bloaters with completed annuli in a single collection decreased as age increased. On 15 June, for example, all III-group fish but none of the VIII-group fish had begun new growth.

The period of annulus formation for Apostle Islands bloaters appears to be similar to that of lake herring (Dryer and Beil, 1964). A few lake herring had begun to grow in early

TABLE 10.—*Age composition of bloaters according to sex, 1958–65*

Year of capture and sex	Number of fish	Percentage in age group										Average age
		I	II	III	IV	V	VI	VII	VIII	IX	X	
1958												
Males	76	–	7.9	15.8	9.2	48.7	11.8	5.3	1.3	–	–	4.6
Females	138	–	0.7	4.3	15.2	25.4	34.1	15.9	2.2	2.2	–	5.6
1959												
Males	34	–	2.9	8.8	20.6	14.7	23.6	11.8	17.6	–	–	5.5
Females	64	–	3.1	4.7	10.9	9.4	25.0	25.0	15.6	6.3	–	6.2
1960												
Males	51	2.0	25.5	2.0	7.8	17.6	11.8	25.5	5.9	2.0	–	4.9
Females	73	–	13.7	–	9.6	16.4	28.7	19.2	11.0	1.4	–	5.5
1961												
Males	56	–	–	7.1	10.7	23.2	30.4	19.6	5.4	3.6	–	5.8
Females	40	–	5.0	12.5	12.5	17.5	27.5	17.5	7.5	–	–	5.3
1962												
Males	23	13.0	–	8.7	21.8	21.8	17.4	8.7	4.3	4.3	–	4.7
Females	97	2.1	–	6.2	13.4	23.6	22.7	13.4	12.4	4.1	2.1	5.8
1963												
Males	66	–	–	–	4.5	10.6	30.3	34.9	10.6	9.1	–	6.6
Females	21	–	–	–	19.0	19.0	43.0	9.5	9.5	–	–	5.7
1964												
Males	56	–	–	7.1	32.1	16.1	28.6	5.4	7.1	3.6	–	5.3
Females	109	–	–	2.8	20.2	25.6	22.9	15.6	9.2	2.8	0.9	5.7
1965												
Males	61	–	–	1.6	4.9	24.6	41.0	19.7	4.9	3.3	–	6.0
Females	113	–	–	–	0.9	17.7	28.2	27.4	20.4	2.7	2.7	6.7
Total or average												
Males	423	1.9	4.5	6.4	14.0	22.2	24.3	16.4	7.1	3.2	–	5.4
Females	655	0.3	2.8	3.8	12.7	19.3	29.1	17.9	11.0	2.4	0.7	5.8
Sexes combined	1,078	1.1	3.7	5.1	13.4	20.7	26.5	17.2	9.1	2.8	0.4	5.6

May, but some had not yet formed an annulus in late July.

Bloaters grew very slowly during the spring and early summer but their growth rate increased sharply in August (Table 8). A graph (not given here) of the average percentages at the bottom of Table 8 was used to obtain estimates of growth within months and at the end of each month (also given at the bottom of Table 8). These estimates were based on the assumption that growth was complete by the end of September.

By the end of July only 30% of the season's growth was complete but by 31 August the fish had completed 80% of the season's growth. Over 50% of the season's growth was completed during August.

Lake herring from the Apostle Islands (Dryer and Beil, 1964) grew more rapidly than bloaters in early summer and had completed over 60% of the season's growth by late July (compared with only 25% for bloaters). By the end of August, however, both lake herring and bloaters had completed over 80% of the season's growth.

Age Composition and Year-class Strength

The age composition of bloaters was characterized by the dominance of age-group VI in nearly every year's collection (Table 9). The VI group dominated the catches except in 1958, 1962 (V group dominant), and 1960 (age-groups VI and VII equally represented). The percentage representation of the VI-group fish ranged from 21.7 in 1962 to 33.5 in 1963 and averaged 26.8%. Fish of age-group V were second in abundance (average percentage, 20.1) and the VII group ranked third (average percentage, 18.9). The oldest bloaters belonged to age-group X. Age composition did not change over the period 1958–65 as the average size of Apostle Islands bloaters increased.

Fluctuations in year class strength were slight during 1958–65. Only two year classes were strong enough to dominate the catch for more than 1 year: the 1953 year class was dominant in 1958 and 1959 and shared dominance in 1960; the 1957 year class was dominant in 1962 and 1963 (Table 9). Of the six year classes (1953–1958) represented successively by age-groups V–VII, all except the year class of 1956 dominated the catch in one or more years.

Records of age composition according to sex (Table 10) show a predominance of males

TABLE 11.—*Sex composition of age groups of bloaters, 1958–65*

Age group	Number of males	Number of females	Percentage of females
I	4	2	33.3
II	20	15	42.9
III	27	23	46.0
IV	53	80	60.2
V	100	135	57.4
VI	105	183	63.5
VII	72	122	62.9
VIII	28	71	71.7
IX	14	18	56.3
X	–	6	100.0
Combined sample	423	655	60.8

in all age groups below VI and of females in age-groups VI through X (exception was the IX group). The average age of the females was higher than that of the males in each year's collection except 1961 and 1963. The mean age of the females for the combined collections was 5.8 (range, 5.3 in 1961 to 6.7 in 1965). The average age of the males ranged from 4.6 in 1958 to 6.6 in 1963 (average, 5.4).

Sex Composition

Sex composition fluctuated irregularly and without trend in 1958–65. The percentage of females in the annual samples ranged from 24.1% in 1963 to 80.8% in 1962. The annual fluctuations may have been affected more by the season of collection than by true annual changes.

In the combined collections, the number of males exceeded females in age-groups I–III but the females outnumbered males in age-groups IV–X (Table 11). The percentage of females increased steadily from 33.3% for age-group I to 60.2% for the IV group. The advantage of the females fluctuated irregularly with age and ranged from 56.3 to 71.7% for age-groups V–IX and was 100% for the six X-group fish.

The predominance of females in collections of coregonines from the Great Lakes is not unusual. In Lake Superior, females dominated in collections of shortjaw cisco (Van Oosten, 1937) and lake herring (Dryer and Beil, 1964), and in Lake Michigan females were dominant in samples of bloaters, collected in 1928 (Jobes, 1949a), longjaw cisco (Jobes, 1949b), shortnose cisco (Jobes, 1943), and kiyi (Deason and Hile, 1947).

TABLE 12.—*Relation between age and sexual maturity of bloaters, 1958–65. [All fish younger than II were immature and all fish older than III were mature]*

Age group and sex	Number immature	Number mature	Percentage mature
II			
Males	36	16	31
Females	36	5	12
III			
Males	3	31	91
Females	4	34	89

The sex composition of Apostle Islands bloaters varied according to month of collection. Although the data are not strictly comparable because the samples came from different mesh sizes in some months, males appeared to outnumber females during February and March and the percentage of females tended to increase during the early summer and reached a peak (about 70%) in July. The percentage of females decreased slightly in the fall.

The monthly changes in sex composition observed in the Apostle Islands agreed well with those in Lake Michigan where Jobes (1949a) reported that the percentage of female bloaters taken in gill nets also increased from spring to summer and decreased in the fall.

Seasonal changes in sex composition probably indicate segregation by sex, or sex differences in activity during different periods of the year. The higher percentage of males during February and March is undoubtedly related to spawning. Males are either more numerous on the spawning grounds or they are more active than females, and thus more vulnerable to stationary gear such as gill nets.

Age and Size at Maturity

Youngest mature Apostle Islands bloaters belonged to age II, and all fish older than age III were mature (Table 12). More males than females were mature at age II but the percentages were nearly equal for the age III group (91% for males, 89% for females).

The smallest mature male bloater was 6.0 inches long and the smallest mature female was 7.0 inches (Table 13). All bloaters longer than 8.4 inches were mature.

TABLE 13.—*Relation between length and sexual maturity of bloaters.* [*All fish shorter than 6.0 inches were immature and all fish longer than 8.4 inches were mature*]

Total length (inches)	Males			Females		
	Number immature	Number mature	Percentage mature	Number immature	Number mature	Percentage mature
6.0–6.4	11	2	15	12	0	0
6.5–6.9	17	3	15	20	0	0
7.0–7.4	15	10	40	8	6	43
7.5–7.9	4	23	85	3	11	79
8.0–8.4	6	64	91	5	39	89

TABLE 14.—*Relation between gonad condition and season, 1958–65*

Date[1]	Number of fish examined	Number ripe	Number spent	Percentage spent
1–28 June (4)	346	1	0	0
6–18 July (2)	323	7	0	0
18–29 Aug. (3)	427	4	0	0
6–18 Sept. (2)	278	0	2	0.7
2–22 Oct. (2)	213	0	4	1.9
16–25 Nov. (2)	383	56	8	2.1
28 Feb.–30 Jan. (1)	503	157	98	19.5
8–31 March (1)	224	58	34	15.2
28 April (1)	124	3	0	0
18 May (1)	107	2	0	0

[1] Figure in parentheses following each time period gives the number of calendar years in which samples were taken.

The data on age and size at maturity were from fish taken in all years, seasons, and gears. The records were not adequate to measure possible year-to-year changes.

Koelz (1929) stated that bloaters from Lake Superior matured at about 158 mm (6.2 inches total length). His observation was made in 1922 on what apparently was a slower growing stock and does not necessarily imply that the fish matured at a younger age than those of this study.

Spawning

Although some ripe bloaters were caught in all months, most spawning in the Apostle Islands region appears to take place in February and March. Spent bloaters were first observed in September (Table 14). The number of spent fish increased progressively each month from September to February (records are not available for December and most of January). The percentage began to decrease in March and by the end of April no spent fish were taken. The presence of ripe individuals in nearly all of the samples, however, suggests that some spawning may take place throughout the year.

Spent and ripe bloaters during the main spawning period (February–March) were taken at depths of 20 to 50 fathoms from nets set on the bottom. The fish apparently had no particular preference for any one of the various bottom types over which the gill nets were set.

The spawning season in Lake Superior during 1958–65 agreed well with that in Lakes Michigan and Huron where Koelz (1929) reported spawning in late February and early March. Jobes (1949a) also indicated that bloaters in Lake Michigan spawn in February and March.

Fecundity

The fecundity of Apostle Islands bloaters was estimated from 20 mature females collected in the fall of 1964–65. The connective tissue was removed from the formalin-preserved ovaries and the eggs were placed on absorbent paper to drain. Four 1-ml samples of the thoroughly drained eggs were counted into a sedimentation tube graduated to 0.01 ml. The average number of eggs in the four samples was multiplied by the total volume of

TABLE 15.—*Relation between the length of bloaters and the total number of eggs and the number per ounce of weight.* [*Number of fish in parentheses*]

Average length[1] (inches)	Number of eggs per fish		Average number of eggs per ounce of fish
	Average	Range	
8.4	4,225[2] (1)	–	1,408
8.8	4,758 (2)	3,116–6,300	1,379
9.2	4,986 (2)	3,822–6,149	1,247
9.7	5,039 (3)	3,727–6,225	1,050
10.3	6,304 (4)	5,323–7,905	1,121
10.7	7,735 (5)	6,387–8,825	1,232
11.1	9,139 (2)	6,233–12,045	1,195
11.7	10,080[2] (1)	–	1,292
All lengths	6,533 (20)	3,116–12,045	1,241

[1] Mean for fish of ½-inch intervals.
[2] Actual count.

TABLE 16.—*Percentage of occurrence and (in parentheses) percentage of total volume of food in stomachs of bloaters according to month. [0.0 indicates less than 0.05]*

Item	Month of collection				Combined samples
	May	June	July	November	
Number of stomachs	50	108	92	72	322
Length of fish (inches)	3.3–11.0	3.2–10.5	6.2–10.6	5.7–11.2	3.2–11.2
Food					
Crustaceans	100.0 (75.4)	100.0 (90.0)	96.7 (95.9)	98.6 (98.6)	98.8 (90.0)
Conchostraca	2.0 (0.0)	– –	1.1 (0.0)	2.8 (0.0)	1.5 (0.0)
Cladocera	– –	– –	– –	23.6 (0.0)	5.9 (0.0)
Copepoda	80.0 (9.9)	96.3 (70.5)	70.7 (18.4)	61.1 (13.9)	77.0 (28.2)
Ostracoda	18.0 (0.0)	– –	7.6 (0.0)	– –	6.4 (0.0)
Mysis relicta	58.0 (56.2)	11.1 (0.8)	26.1 (8.5)	70.8 (84.7)	41.5 (37.5)
Pontoporeia affinis	16.0 (9.3)	25.9 (18.7)	30.4 (69.0)	1.4 (0.0)	18.4 (24.3)
Insects	12.0 (0.0)	34.3[1] (0.6)	19.6 (0.7)	4.2 (0.1)	17.5[1] (0.4)
Diptera	10.0 (0.0)	– –	3.3 (0.0)	4.2 (0.1)	– –
Homoptera	– –	– –	2.2 (0.7)	– –	– –
Unidentified insects	2.0 (0.0)	– –	– –	– –	– –
Sphaeriidae	16.0 (1.2)	2.8 (0.0)	13.0 (0.7)	12.5 (0.1)	11.1 (5.0)
Fish eggs	6.0 (0.6)	– –	– –	– –	1.5 (0.2)
Unidentified debris	4.0 (22.8)	12.0 (9.4)	8.7 (2.7)	2.8 (1.2)	6.9 (9.0)

[1] Insects were not identified in the June collection.

the eggs in the ovaries to provide an estimate of the total number of eggs.

The number of eggs increased with fish length (Table 15). The average number rose from 4,225 for an 8.4-inch bloater to 10,080 for a 11.7-inch fish. The average number of eggs per ounce of body weight decreased from 1,408 for the 8.4-inch fish to 1,050 for fish 9.7 inches long, and fluctuated between 1,121 and 1,292 for fish longer than 9.7 inches. The mean diameter of 160 eggs (20 from each of 8 bloaters, 10.1–11.2 inches long) was 1.95 mm (range, 1.86 to 2.01 mm).

Comparisons between the number of eggs produced by bloaters and lake herring (Dryer and Beil, 1964) of the same length reveal that bloaters produce about 60% more eggs than lake herring. A 10.7-inch bloater, for example, produced 7,735 eggs compared with 4,314 eggs for a lake herring of the same length. The average number of eggs per ounce of body weight was also higher (about 30%) for bloaters.

Food of Bloaters

Stomachs were examined from 322 bloaters captured in the Apostle Islands region in May, July, and November 1965 and June 1966. Quantitative measures were made by liquid displacement in a sedimentation tube graduated to 0.01 ml.

Crustaceans were the most common food (Table 16). They were present in nearly all the stomachs examined, and composed 90% of the total volume in the combined samples. Copepods ranked first in frequency of occurrence (77%), followed by *Mysis* and *Pontoporeia*. *Mysis* made up the greatest volume (37.5%), followed by copepods and *Pontoporeia*. Insects were found in 17.5% of the stomachs but composed less than 1% of the total volume.

With few exceptions, seasonal differences in the food of bloaters were small. The importance of *Pontoporeia* increased steadily from May to July but declined to insignificance in

November. The percentage of total volume contributed by *Mysis* was highest in May and November (56 and 85%, respectively) and lowest in June and July. Copepods were most important in June (70% of total volume) and least common in May (10% of volume).

The occurrence of fingernail clams and fish eggs suggests occasional bottom feeding, but the main food indicates that bloaters are primarily pelagic feeders.

A comparison of foods between large and small bloaters (8 inches and above; below 8 inches) revealed that copepods composed 98% of the total volume for small bloaters and 43% for the larger fish. *Pontoporeia* contributed 46% of the volume of food for the larger fish and only 1% for fish shorter than 8 inches. *Mysis* were found in the stomachs of 17% of the larger fish and 7% of the smaller fish.

The food of Apostle Islands bloaters was very similar to that found by Wells and Beeton (1963) in bloaters of Lake Michigan. Zooplankton was the main food of bloaters under 7 inches and *Pontoporeia* and *Mysis* were most common in fish larger than 7 inches. In contrast to the present study, Wells and Beeton found that the incidence of *Pontoporeia* increased and that of *Mysis* decreased as the fish size increased.

Koelz (1929) reported that bloaters from 30 fathoms or less in Lake Huron ate principally *Pontoporeia* and almost all stomachs contained *Pisidium.* Stomachs of the deepwater fish (60 fathoms and deeper) contain mostly *Mysis.*

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Rehabilitation of Lake Trout in the Apostle Islands Region of Lake Superior[1,2]

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ABSTRACT

Marked success of rehabilitation of lake trout in Lake Superior has been due principally to the control of the sea lamprey and closure of the lake trout fishery in 1962 and large-scale plantings of yearling lake trout in 1959–66. After the sea lamprey became established in the late 1940s, spawning stocks of lake trout began to decrease and were almost nonexistent by 1960–61. After control of the sea lamprey and closure of the commercial fishery for lake trout in 1962, the abundance of spawning stocks began to rise and reached the highest levels on record in 1964–66. Successful spawning in 1964 and 1965 was demonstrated by catches of age-0 lake trout in 1965 and 1966, the first evidence of natural reproduction since 1959.

Plantings of hatchery-reared lake trout in Wisconsin waters of Lake Superior began in 1952. The percentage of hatchery-reared fish in catches of juvenile lake trout increased almost steadily from 1953 to 1965 (when nearly all were of hatchery origin). The abundance of juvenile fish increased from 1959 to 1962 and remained nearly constant in 1962–66. The success of lake trout plantings was highest in 1959–61 but generally declined after 1961; the success of the plantings was inversely related to the abundance of older lake trout.

Annual increments of growth of hatchery-reared lake trout varied from 1.1 to 5.0 inches after planting. The average lengths of fish of identical age-groups varied according to gear of capture, depth of water, and season. More than 65% of the season's growth of age-III lake trout took place after September.

The findings indicated that the present rate of stocking lake trout may be higher than necessary to maintain optimum abundance.

INTRODUCTION

Rehabilitation of lake trout (*Salvelinus namaycush*) in the Apostle Islands region of Lake Superior has been highly successful due to the control of the sea lamprey (*Petromyzon marinus*), closure of the commercial fishery for lake trout, and the large-scale plantings of yearling (14- to 20-month-old) lake trout by the State of Wisconsin.

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In 1962, after the 87% reduction in the catches of spawning sea lampreys at all electrical assessment barriers in Lake Superior (Great Lakes Fishery Commission, 1964) and the closure of the commercial fishery for lake trout, the Bureau of Commercial Fisheries and the Wisconsin Conservation Division increased their efforts to monitor changes in lake trout stocks. Information was needed on the proper size, season, and location for planting lake trout (Pycha and King, 1967), dispersal of the fish after planting (Pycha et al., 1965), efficient stocking rates, and the relative success of various hatchery plants. Needed also was information on the status of spawning stocks and evidence of natural reproduction.

This report describes the changes in spawning stocks, the effects of hatchery plantings on stocks of juvenile lake trout, the success of various plantings, the re-establishment of natural reproduction, and the growth of hatchery-reared lake trout.

MATERIALS AND METHODS

This study is based primarily on 15,651 lake trout taken in 1958–66 in experimental bottom trawls and small- and large-mesh gillnets fished by the Bureau of Commercial Fisheries research vessel *Siscowet* (Table I), and 12,381 lake trout caught in 4.5-inch mesh (extension measure) gillnets by Wisconsin commercial fishermen under special permit with the State. Records were also used of fish taken by the Wisconsin Conservation Division on the lake trout spawning grounds in 1951–60. All of the fish were taken in the Apostle Islands region of Lake Superior. Hatchery-reared lake trout were identified by fin marks used for the various plantings.

Sampling Gear and Fishing Methods

The bottom trawls were semiballoon with a 31-ft headrope, 2-inch mesh (extension measure) cotton body, and 0.5-inch mesh codend. Trawls were dragged along the bottom contour for 15 min at 3 miles per hour. A total of 557 tows were made, of which 344 were at four stations for systematic trawling.

The small-mesh nylon gillnets, 300 ft long and 6 ft deep, were fished in 12 net gangs. Each gang consisted of two nets of each mesh size from 2 to 3 inches, by 0.25-inch intervals, and 3.5-inch mesh. The nets were set along the bottom contours and fished for 48 hr. Nets of various meshes were randomly distributed within a gang. A total of 911,900 linear ft of small-mesh gillnets were fished, of which 621,800 ft were fished at three gillnet stations.

The gangs of large-mesh gillnets fished on the lake trout spawning grounds by the *Siscowet* usually consisted of 13 nets 275 ft long and had mesh sizes from 4.5 to 6 inches. The usual number of nets of the various mesh sizes fished in a gang was: 4.5-inch mesh, 2; 5-inch, 3; 5.5-inch, 4; and 6-inch, 4. Occasionally 150 ft each of 1.5- and 2.5-inch mesh nets were attached to the gang to collect smaller species suspected of preying on lake trout eggs. (Of the several hundred stomachs examined from longnose suckers, *Catostomus*

TABLE I. Numbers of juvenile lake trout captured with different gears by the R/V *Siscowet*, and percentages of hatchery origin (finclipped), in the Apostle Islands region of Lake Superior, 1958–66.

	Trawls			Small-mesh gillnets			Large-mesh gillnets		
Date	No. of tows	No. of fish	Percentage finclipped	Feet of net fished (*thousands*)	No. of fish	Percentage finclipped	Feet of net fished (*thousands*)	No. of fish	Percentage finclipped
1958	–	–	–	73.8	119	20.2	–	–	–
1959	58	73	55.3[a]	37.4	131	34.4	–	–	–
1960	66	85	75.4	148.5	181	33.7	–	–	–
1961	89	442	95.7	17.9	53	75.5	34.8	17	0.0
1962									
Spring	15	202	95.0	5.3	11	81.8	–	–	–
Summer	–	–	–	2.4	3	100.0	–	–	–
Fall	28	452	99.1	4.8	30	90.0	–	–	–
All seasons	43	654	98.2	12.5	44	88.6	57.4	100	0.0
1963									
Spring	48	654	98.9	23.0	268	91.4	–	–	–
Summer	–	–	–	41.6	440	94.3	–	–	–
Fall	32	440	99.5	38.8	390	90.0	–	–	–
All seasons	80	1094	99.1	103.4	1098	92.1	60.3	235	1.3
1964									
Spring	31	558	98.6	57.6	996	98.5	–	–	–
Summer	–	–	–	57.6	556	96.8	–	–	–
Fall	36	794	99.7	57.6	564	96.1	–	–	–
All seasons	67	1352	99.2	172.8	2116	97.4	17.6	626	3.9
1965									
Spring	40	440	99.1	57.6	695	97.3	–	–	–
Summer	–	–	–	57.6	574	98.6	–	–	–
Fall	37	601	98.7	57.6	678	97.2	–	–	–
All seasons	77	1041	98.9	172.8	1947	97.6	17.9	683	6.6
1966									
Spring	42	468	98.5	57.6	911	98.6	–	–	–
Summer	–	–	–	57.6	756	98.5	–	–	–
Fall	35	267	94.8	57.6	720	98.5	–	–	–
All seasons	77	735	97.2	172.8	2387	98.5	22.2	438	12.3
Total	557	5476	–	911.9	8076	–	210.2	2099	–

[a] Percentage based on 47 fish (26 were not examined for clipped fins).

catostomus, lake herring, *Coregonus artedi*, round whitefish, *Prosopium cylindraceum*, burbot, *Lota lota*, and lake northern chubs, *Hybopsis plumbea plumbea*, only one lake trout egg was found — in a longnose sucker.)

Gillnets fished by the Wisconsin Conservation Division on the spawning grounds in 1951–60 were of 5- to 7.5-inch mesh. The 6.5-inch mesh was most commonly used.

Seven "index" stations were selected for systematic fishing with trawls or small-mesh gillnets (Fig. 1). The criteria used in the selection of the stations included bottom type and topography, geographical location in relation to lake trout planting sites, and abundance of juvenile lake trout.

The four trawl stations were fished in the spring and fall, 1962–66, except that the Michigan Island station was fished only in the fall for native young-of-the-year lake trout. At least ten 15-min tows were made at each station during each season.

The three gillnet stations were fished in the spring, summer, and fall, 1963–66. Beginning in 1964, 21,600 ft of small-mesh gillnets (3600 ft of each mesh size) were fished during each season at the stations west of Madeline Island and south of Stockton Island, and 14,400 feet (2400 ft of each mesh size) were fished at the station east of Madeline Island. The total length of net of some mesh sizes was less in 1963 than in other years due to lack of gear.

As part of an interagency study to determine the survival of age-0 lake trout planted in the fall and age-I fish planted in the spring,[3] the Wisconsin Conservation Division in 1950 issued permits to five commercial fishermen to collect lake trout eggs in the Apostle Islands region for rearing in the Salmo Hatchery at Bayfield, Wisconsin. The annual collection of eggs continued under the State's supervision through 1960. Most of the fishing was on Gull Island Shoal, one of the major lake trout spawning areas in Wisconsin waters (Fig. 1). Egg collections by the State were discontinued after 1960 because the catches of spawning fish had become too small to provide the required number of eggs.

Beginning in 1961 the *Siscowet* fished Gull Island Shoal to assess changes in abundance of spawning lake trout. The number of sets on the shoal depended mainly on weather and abundance of spawning fish. The total length of large-mesh nets fished on the shoal in 1961–66 ranged from 17,600 ft in 1964 to 60,300 ft in 1963.

Collection and Analysis of Data

Lake trout caught in trawls and small-mesh gillnets were examined for clipped fins, measured (total length in inches), and returned to the water if alive. In 1962–65 the anal fin was removed from all lake trout returned to the water to determine the number of fish recaptured in later tows or in gillnet

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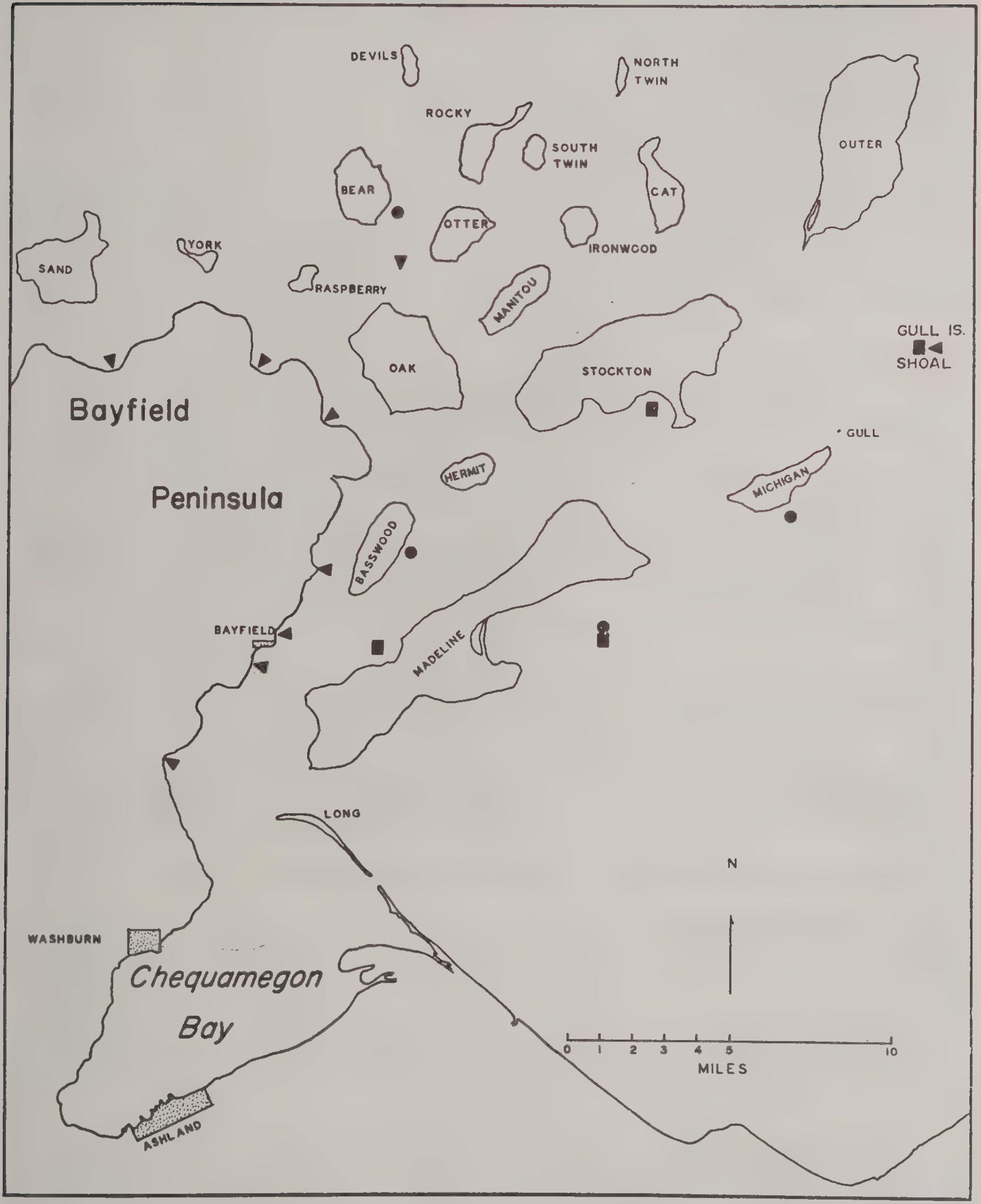
[3] Returns of yearlings planted in the spring were 9–10 times greater than returns of fingerlings planted in the fall. Reviews of this study were given by Buettner (1961), Pycha et al. (1965), and Pycha and King (1967).


DEVILS
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OUTER
BEAR
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OTTER
IRONWOOD
SAND
YORK
RASPBERRY
MANITOU
GULL IS. SHOAL
OAK
STOCKTON
Bayfield
Peninsula
GULL
HERMIT
MICHIGAN
BASSWOOD
BAYFIELD
MADELINE
LONG
N
WASHBURN
Chequamegon
Bay
0 1 2 3 4 5 10
MILES
ASHLAND

FIG. 1. Apostle Islands region of Lake Superior, showing index trawl stations (circles), index gillnet stations (squares), and lake trout planting sites (arrows).

sets. The number of anal-clip returns, however, was so small (less than 2%) that the practice was abandoned. The small return indicated either poor survival of the released fish or extremely high abundance of fish on the fishing grounds.

Information on lake trout from commercial gillnets was provided by the Wisconsin Conservation Division. The Division used its own vessel in 1962 and issued permits to three commercial fishermen in 1963–66 to fish a limited amount of gear at specified locations during April–May, August–September, and November–December.

Although finclipped lake trout have been planted in Wisconsin waters of Lake Superior every year since 1952 (except in 1957), the present study deals only with plantings in 1959–66 (Table II). The annual plantings varied from 151,000 fish in 1959 to more than 743,000 in 1964. The size of the fish at release ranged from 8.9 to 26.5 fish per pound.

TABLE II. Lake trout planted in the Apostle Islands region, 1959–66.

Year-class and mark	Date planted	No. planted	No. per pound
1958			
RPRM (right pectoral–right maxillary)	May 11–21, 1959	75,500	22.0
ARP (adipose–right pectoral)	"	75,500	21.8
1959			
LP (left pectoral)	May 11–13, 1960	161,350	20.0
1960			
A (adipose)	May 31–June 2, 1961	109,000	26.5
DRV (dorsal–right ventral	"	108,000	22.0
1961			
ABV (adipose–both ventrals)	May 7–31, 1962	255,500	17.7
DLP (dorsal–left pectoral)	June 14–26, 1962	120,800	22.5
DLV (dorsal–left ventral)	Sept. 24–Oct. 11, 1962	115,870	8.9
1962			
LPRV (left pectoral–right ventral)	Mar. 12–May 21, 1963	311,469	18.8
1963			
ARP (adipose–right pectoral)	Jan. 8–May 11, 1964	743,435	22.1
1964			
A (adipose)	Jan.–May, 1965	347,450	19.8
1965			
DLV (dorsal–left ventral)	Jan. 21–May 19, 1966	351,870	25.2

Some annual plantings during this period were omitted from the analyses because of unusually small returns or differences in planting locations. The 1962 fall planting of 115,870 fish, for example, was omitted from the trawl analysis because the fish were unusually large when planted and probably were not fully vulnerable to the trawl.

With the exception of the 1958 year-class, planted in 1959, all lake trout were planted from shore at various sites along the Bayfield Peninsula (Fig. 1). The 1959 releases were made by boat at the two offshore planting sites. The fish planted each year were divided about equally among the shore sites.

Estimates of the relative success of various hatchery plantings were based on the catch per unit of effort (CPE) for trawls and small-mesh gillnets at index stations and for commercial gillnets fished by cooperating commercial fishermen. The units of effort were 10 tows (15 min each) for trawls and 100,000 linear ft for small-mesh and commercial gillnets. Abundance indices on which we based our estimates were the catches (numbers of fish) per unit of effort adjusted through multiplication by the reciprocal of the size of the planting. To avoid small decimal values this figure was in turn multiplied by 10^5. Abundance indices were calculated individually for each plant at each station, season, and (for gillnets) by mesh size. The unweighted mean of seasonal values for each gear was used as the annual abundance index.

Estimates of abundance of fish on the spawning grounds was based on the number of fish caught per 10,000 ft of large-mesh gillnets. The number of feet of large-mesh nets fished on the spawning grounds was considerably less than that for small-mesh and commercial gillnets.

The study of growth of hatchery-reared lake trout was based on the average lengths at capture of fish of different age-groups collected in May 1962–66, before annual growth had resumed. Ages were assigned on the basis of fin marks (Table II) used for the various plantings. Although fin regeneration or faulty marking may have caused errors in age assignments, we believe that errors were negligible.

Age determinations of the native spawning-run lake trout were made from scales by the staff at the U.S. Bureau of Commercial Fisheries Biological Station at Ashland, Wisconsin. Although late onset of growth made age determinations difficult in some years, enough known-age (finclipped) fish were read correctly to give confidence in the age determinations for native fish.

CHANGES IN SPAWNING STOCKS

The major objective of the lake trout rehabilitation program on Lake Superior is to re-establish spawning stocks to a level capable of sustaining the population by natural reproduction. Early progress toward success of this objective was evidenced in Wisconsin waters in the fall of 1964 by a remarkable increase in the number of spawning fish, and in the summers of 1965–66 by the presence of naturally spawned (native) young of the year. Lake trout also reproduced successfully in the fall of 1965 and 1966.

Changes in Abundance

The abundance of spawning lake trout in the Apostle Islands region declined sharply from 1952 to 1953, rose slightly in 1955, and then declined almost steadily to 1960 when the catch per unit of effort (CPE) was only 3 males and 0.7 female per 10,000 ft of gillnets (Table III, Fig. 2). The CPE for males increased to 5 in 1961 but no females were captured. Abundance of spawning fish increased slowly in 1962–63 but in 1964 the CPE for males increased to the highest level since 1951 and that for females to the highest

TABLE III. Numbers of spawning lake trout captured per 10,000 ft of large-mesh gillnets on Gull Island Shoal, 1951–66, and of sea lampreys taken from electrical barriers on five streams tributary to Lake Superior.

	Year and (in parentheses) thousands of feet of gillnets lifted															
Species	1951 (60)[a]	1952 (28)	1953 (54)	1954 (60)[a]	1955 (60)	1956 (60)[a]	1957 (60)[a]	1958 (80)	1959 (105)	1960 (61)	1961 (35)	1962 (57)	1963 (60)	1964 (18)	1965 (18)	1966 (22)
Lake trout																
Males	68	94	11	16	42	26	24	29	20	3	5	16	34	310	341	154
Females	31	74	14	15	34	14	15	8	3	0.7	0	0.5	3	42	41	44
Sea lampreys (*thousands*)[b]	–	–	1.4	2.7	3.1	8.0	13.0	6.6	8.2	12.9	13.3	2.7	3.8	2.3	2.2	1.4

[a] Approximately 60,000 ft.

[b] Based on the annual catches of spawning sea lampreys at electrical barriers on the Betsy, Two Hearted, Sucker, and Miners rivers, and Furnace Creek. These were the only streams for which complete catch records were available for 1953–66.

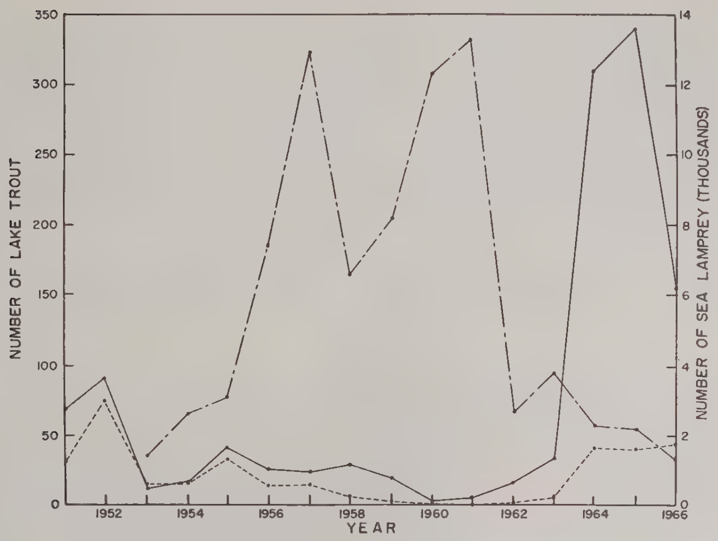

FIG. 2. Average numbers of spawning lake trout (males, solid line; females, short dashes) caught per 10,000 ft of gillnets fished on Gull Island Shoal, and numbers of adult sea lampreys (long and short dashes) taken at electrical barriers in five streams on the south shore of Lake Superior. (For names of streams and basis for selection, see Table III, footnote *b*.)

point since 1952 (310 males and 42 females per 10,000 ft of net). The CPE for males increased further in 1965 to 341 fish but dropped in 1966 to 154. The CPE for females remained about the same in 1964–66.

Age determinations revealed that native fish of year-classes 1957–59 were mainly responsible for the remarkable increase in spawning fish in 1964–65. Lack of recruitment to age-groups below VII contributed to the decline in abundance of males in 1966. The decline might also reflect the timing of the fishing in relation to the peak of spawning. A possibility exists that the peak of the spawning run was missed in 1966 and many of the males may have left the grounds before fishing began.

Although the mesh sizes fished in 1961–66 were slightly smaller and perhaps more efficient than those fished in 1951–60, the records show without question that spawning fish were practically nonexistent in 1960–61 and were abundant in 1964–66.

The changes in abundance of mature lake trout were inversely related to the abundance of sea lampreys in Lake Superior (Table III, Fig. 2). During the years of highest lamprey abundance (1956–61), stocks of spawning lake trout declined and reached the lowest level in 1961 when sea lamprey abundance was highest. After the 87% reduction in catches of sea lampreys at all 29 electrical barriers on Lake Superior (Great Lakes Fishery Commission, 1964) and the closure of the commercial lake trout fishery in U.S. waters of the lake in 1962, mature lake trout stocks began to increase.

Although little question exists that the sea lamprey was an important factor in the decline of spawning lake trout, other factors apparently contributed to the lower abundance in the early 1950's than in the middle 1960's. Abundance of sea lampreys in 1953 (the first year of record) was lower than in 1964–65 when spawning stocks were abundant. Had the sea lamprey been the only factor affecting abundance of mature lake trout, the size of spawning stocks in the early 1950's should have been as high as or higher than in 1964–66. The closure of the commercial fishery may have been largely responsible for the greater abundance in the middle 1960's.

CHANGES IN BIOLOGICAL CHARACTERISTICS

The decline and subsequent increase in abundance of lake trout on the spawning grounds were accompanied by changes in sex ratios, average lengths, and age distributions of the spawning stocks.

The percentage of females fluctuated between 31 and 56% in 1951–57 but began to decline in 1958 and reached zero in 1961 (Fig. 2). The percentages began an irregular increase in 1962 and reached 22% in 1966 — the highest since 1958.

The average lengths of spawning lake trout (Table IV) decreased with the decline in abundance and increased as the fish became more plentiful. The average lengths of the males decreased from 27.8 inches in 1957 to 25.4 inches in 1961, when abundance of the spawning stocks was lowest. As abundance began to increase in 1962 the average lengths of the males increased and reached 27.2 inches in 1966, the highest since 1957. Average lengths of the females followed similar trends; females were longest (32.4 inches) in 1957, declined to 28.0 inches in 1963, and increased to 29.4 inches in 1964 and 1966.

The age distributions of the spawning-run lake trout changed considerably over the period for which records are available (Table V). The most obvious change was the shift from old to young fish during the period of decline and the gradual increase in numbers of older fish during the years of recovery. Although no scales were collected from spawning lake trout in the Apostle Islands region before 1957, a sample taken near Marquette, Michigan, in 1953 (Rahrer, 1967), gives a general idea of the age composition of spawning-run lake trout before the sea lamprey became firmly established in Lake Superior (Table V). The mean ages of spawning lake trout were 9.8 for males and 10.4 for females. Most of the males were of ages IX and X and the females, X and XI. No fish younger than age VII were taken. In 1957 the mean age of Wisconsin fish was 8.6 for males and 10.0 for females. By 1961 the average age of the males had dropped to 6.0 (no females were taken) and in 1963 the mean ages were 6.7 for males and 7.5 for females. Most of the males were in age-groups VI and VII and none were older than IX. The presence of younger spawning fish may reflect faster growth, which can result in earlier maturity.

After 1963 the mean ages of the fish gradually increased and by 1966 the averages were 7.8 for males and 8.0 for females. The percentage contribution had declined for age-groups below VII and increased for age-groups above VIII.

TABLE IV. Length distributions of spawning-run lake trout from the Apostle Islands region, 1957–66. Fish were not measured in 1960; no females were captured in 1961.

Total length (*inches*)	Males									Females							
	1957	1958	1959	1961	1962	1963	1964	1965	1966	1957	1958	1959	1962	1963	1964	1965	1966
20.0–20.9	–	–	–	–	–	2	–	1	–	–	–	–	–	–	–	–	–
21.0–21.9	–	–	1	–	1	1	–	5	–	–	–	–	–	–	–	–	–
22.0–22.9	8	–	5	2	6	6	14	14	8	–	–	–	–	–	–	–	–
23.0–23.9	16	23	11	3	3	9	41	44	15	–	–	–	–	–	–	2	–
24.0–24.9	16	28	19	3	22	30	75	66	36	–	–	–	–	–	–	1	1
25.0–25.9	24	58	36	4	21	33	96	100	42	–	5	2	–	3	2	1	7
26.0–26.9	36	30	41	1	21	37	99	117	70	–	1	6	–	6	5	11	5
27.0–27.9	40	28	43	2	10	44	89	85	53	7	6	2	–	6	8	11	10
28.0–28.9	53	30	16	–	7	30	80	69	38	13	12	2	1	7	16	17	14
29.0–29.9	32	5	13	1	5	9	43	51	37	38	6	6	2	5	11	17	15
30.0–30.9	4	9	8	1	1	4	9	27	21	13	6	5	–	3	24	3	17
31.0–31.9	20	7	5	–	–	–	2	19	12	7	7	1	–	–	7	9	17
32.0–32.9	8	7	4	–	–	–	3	9	6	7	6	2	–	–	–	1	3
33.0–33.9	4	2	–	–	–	–	–	2	2	7	4	1	–	–	1	1	7
34.0–34.9	8	2	–	–	–	–	–	–	1	26	5	1	–	–	1	–	–
35.0–35.9	–	4	1	–	–	–	–	–	–	32	2	1		–	–	–	–
36.0–36.9	–	2	3	–	–	–	–	–	–	7	4	–	–	–	–	–	1
37.0–37.9	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–
38.0–38.9	–	–	–	–	–	–	–	–	–	7	2	–	–	–	–	–	–
Total	269	235	206	17	97	205	551	609	341	164	67	30	3	30	75	74	97
Avg length	27.8	26.5	26.5	25.4	25.9	26.4	26.5	26.8	27.2	32.4	30.5	29.1	29.2	28.0	29.4	28.6	29.4

TABLE V. Age compositions of spawning-run lake trout in Lake Superior off Marquette, Michigan, in 1953 and in the Apostle Islands region in 1957 and 1961–66.

Year and sex	No. of fish	Percentage in age-group										Avg age
		IV	V	VI	VII	VIII	IX	X	XI	XII	>XII	
1953[a]												
Males	142	–	–	–	0.7	2.2	29.6	44.4	18.5	4.4	–	9.8
Females	48	–	–	–	–	–	12.5	41.7	39.6	6.2	–	10.4
1957												
Males	269	–	–	–	17.9	35.7	32.1	7.1	–	3.6	3.6	8.6
Females	164	–	–	–	–	–	50.0	25.0	4.2	16.7	4.2	10.0
1961												
Males	17	–	27.6	58.6	6.9	3.4	3.4	–	–	–	–	6.0
Females	0	–	–	–	–	–	–	–	–	–	–	–
1962												
Males	97	4.2	18.9	29.5	37.9	8.4	1.1	–	–	–	–	6.3
Females	3	–	–	–	33.3	33.3	33.3	–	–	–	–	8.0
1963												
Males	205	–	8.8	32.2	36.6	21.5	1.0	–	–	–	–	6.7
Females	30	–	3.3	6.7	30.0	60.0	–	–	–	–	–	7.5
1964												
Males	551	–	4.3	32.4	50.0	10.9	2.4	–	–	–	–	6.7
Females	75	–	–	4.0	41.3	41.3	12.0	1.3	–	–	–	7.7
1965												
Males	609	–	5.1	29.7	33.5	19.5	11.0	1.0	0.2	–	–	7.1
Females	74	–	–	4.0	40.5	35.1	18.9	1.4	–	–	–	7.7
1966												
Males	341	–	1.5	7.6	30.5	36.1	17.6	6.5	0.3	–	–	7.8
Females	97	–	–	5.6	25.0	42.0	17.0	9.1	1.1	–	–	8.0

[a] Data from Rahrer (1967).

The changes in sex ratio, length, and age of the spawning lake trout were undoubtedly related to sea lamprey predation. The larger (and hence older) fish were most vulnerable to lamprey attacks and disappeared first. Numbers of females were reduced more rapidly than males, presumably because they mature at a greater size and age than males. After control of the sea lamprey in 1962, more young fish survived to maturity and more of the mature fish survived to spawn in subsequent years.

The 80% decrease in 1966 of age-groups V and VI (1961 and 1960 year-classes) gives evidence that spawning success was poor in 1959 and 1960. These observations were well supported by catches of native young-of-the-year lake trout by the *Siscowet*. Before 1965 the last young-of-the-year lake trout were taken in 1959, when three fish were captured off the west side of Outer Island (Fig. 1). Despite intensive trawling on grounds where age-0 lake trout were caught in 1953 or 1959 (the only years before 1960 during which trawling was carried out), none were captured in 1960–64.

Abundance of spawning stocks on Gull Island Shoal may decline unless hatchery-reared fish replace the weak or nonexistent year-classes of 1960–64 (Table III). It appears doubtful, however, that hatchery-reared lake trout will fully replace the native stocks. Evidence from fishing near the planting sites indicates that hatchery-reared lake trout spawn near the area of planting. In 1966, up to 75% of spawning lake trout from grounds near the planting sites were hatchery fish, whereas only 12% of the lake trout on Gull Island Shoal were hatchery reared.[4] The contribution of hatchery fish on Gull Island Shoal is too small to offset fully the lack of recruitment of younger native spawning lake trout.

The success of spawning in 1964 and 1965 was demonstrated by catches of young-of-the-year lake trout in 1965 and 1966. Bottom trawls fished in late summer and fall of 1965 captured 76 young of the year on grounds south of Michigan Island. In addition, four were taken on inshore grounds near the planting sites. The catch of 31 young-of-the-year lake trout at the Michigan Island station in 1966 gives evidence that spawning in 1965 was also successful.

CHANGES IN JUVENILE LAKE TROUT STOCKS

The percentage of hatchery-reared fish in catches of juvenile lake trout in the Apostle Islands region increased almost steadily from 1953 (the first year for which records are available) to 1965. Plantings of finclipped lake trout in Wisconsin waters of Lake Superior began in the spring of 1952 when 102,000 marked yearlings were released in the Apostle Islands region. Over 4.2 million finclipped lake trout were planted in Wisconsin waters in 1952–66.

Although the 1953–57 records are scanty and not entirely comparable with those of the present study, they provide a general idea of the buildup of hatchery fish. The Bureau of Commercial Fisheries R/V *Cisco* in 1953 captured 35 juvenile lake trout in the Apostle Islands region, of which 18 (51%) were finclipped. The first records for the *Siscowet* from this region came from gillnets fished in 1958 (Table I). Of 119 lake trout captured, 20% were of hatchery origin. The first dependable records from trawls fished by the *Siscowet* are for 1959 when 55% of 47 fish were hatchery reared. The percentage of hatchery-reared fish in the trawl catches climbed rapidly in the early 1960's and reached nearly 100% in 1965. The slight decline to 97% in 1966 was influenced by the catch of eight native yearling lake trout (1965 year-class).

Although the data from the *Siscowet* in 1959–61 are not strictly comparable with those of 1962–66, the records from trawls suggest that abundance of juvenile lake trout was considerably lower in the earlier than in the later period. The catch per 15-min tow was 1.3 in 1959 and 1960, and increased to 5.0 in 1961 and to 15.0 in 1962. The CPE did not change markedly in 1962–66. The numbers of fish caught per 15-min tow and per 1000 ft of small-mesh gillnets fished at index stations were:

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[4] Since completion of this report we were informed by the staff of the Ashland Biological Station that the percentage of hatchery-reared lake trout on Gull Island Shoal in 1967 increased to 27%.

Year:	1962	1963	1964	1965	1966
Trawls	15	14	20	14	9
Small-mesh gillnets	–	11	12	11	14

Because the fishing was only at index stations the catches would not necessarily measure changes in other areas.

SUCCESS OF HATCHERY PLANTINGS, 1959–66

In the computation of abundance indices for lake trout from different plantings made in 1959–66 (Table VI), numbers of fish caught per unit of effort were estimated for certain age-groups for which data were lacking. The estimates were based on the ratios of the average numbers of fish recaptured at different ages from all available data for a particular gear. Records from trawl catches, for example, indicated that the average number of lake trout from all plantings taken at age II was about 2.5 times the average number taken at age III. Missing data from trawls for certain groups at age II, therefore, were estimated to be 2.5 times the actual catch at age III. All other estimates were derived similarly.

The selectivity of the various gears affected the age composition of the catches. Trawls were most effective for hatchery fish of age-group II, small-mesh gillnets for the III group, and commercial gillnets for age-groups V and VI. Estimates of the relative success of the various plantings (Fig. 3), therefore, were based on the best represented age-groups from the various gears. The data for age-group V were used for commercial gillnets because they included a longer series than age-group VI.

Table VI and Fig. 3 give evidence that the relative success of lake trout planted in the Apostle Islands region has generally declined since 1961. The plantings of 1960 and 1961-A (1961 fish with adipose fin clip) were by far the most successful of all releases made in 1959–65. The success of the two plantings in 1959 and the 1961-DRV group was about average, but the success of the plantings in 1962–65 declined. Early returns in trawls of fish planted in 1966 were the lowest on record (Table VI).

The close agreement among the three types of sampling gear gives confidence in the reliability of the estimates of relative success for the various plantings. Agreement between small-mesh and commercial gillnets was close for all plantings (Fig. 3) but the trawl data for fish from the 1961-A release indicated a lower survival than indicated by the gillnet catches.

Possible Factors Affecting Success

Reasons for the decline in success of plantings after 1961 are not clear. The increased abundance of legal-sized (17.0 inches or longer) lake trout in recent years may be a contributing factor. Analysis of the catch statistics for assessment fishermen in Wisconsin waters indicates that abundance of legal-sized lake trout has increased steadily since 1960. The abundance indices,[5] although strongly biased by low production in 1962–66 (production was limited to that needed for biological assessment), offer some indication of abundance of legal-sized lake trout during the period. The indices, given below, are expressed as percentages of the 1929–43 mean in adjacent Michigan statistical district S-2. Available data indicate that the quality of fishing in Wisconsin was very similar to that in district S-2.

Year:	1959	1960	1961	1962	1963	1964	1965	1966
Percentage of the 1929–43 mean	31	25	27	48	55	70	80	92

When abundance was extremely low in 1959–61 the success of the plantings was high but as abundance increased after 1961, the success of the releases declined. Competition for space and food, and predation by the larger lake trout may have reduced the survival of planted fish.

Comparisons between the number of fish in a planting and its relative success in later years (based on age-III fish from small-mesh gillnets) indicated that the large planting of 1962-ABV and the large releases of 1963–64 were less successful than the smaller plantings of 1959–61 (Table VI). The success of two nearly equal plantings of 1961, however, differed greatly and the small paired releases of 1959 were far less successful than the 1960 planting, which was more than twice as large.

Pycha and King (1967) found that the success of hatchery plantings of lake trout varied with the average size of the fish at planting. Groups of fish 21 per pound or larger were far more successful than those of smaller average size. The present study, however, showed no clear relation between the average size of the fish at planting and survival during the following 4 years. Of the five groups of fish larger than 21 per pound (Table II), only one (1960 planting) had better than average success, whereas the 1961-A release of relatively small fish (26.5 per pound) proved to be one of the most successful. Furthermore, the 1962-DLV fall planting of exceptionally large fish (8.9 per pound) experienced relatively poor success.

Pycha and King (1967) suggested that the high survival of the 1961-A release may have been the result of natural culling of the weaker fish by disease before planting. Buettner (1961) also found that lake trout which had suffered heavy mortality by disease before planting appeared to survive better than fish that suffered only average mortality in the hatchery.

The failure of the present study to show a relationship between survival and average size at planting may be due to the smaller differences in

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[5] Abundance indices were computed by Richard L. Pycha (manuscript in preparation), Bureau of Commercial Fisheries Biological Station, Ashland, Wisconsin.

TABLE VI. Abundance indices, at different ages, of hatchery-reared lake trout from various plantings and (in parentheses) the average numbers caught per 10 trawl tows or per 100,000 ft of gillnets at index stations in the Apostle Islands region.

Age-group	Year of planting, mark,^{a} and (in brackets) number planted												
	1959		1960	1961		1962			1963	1964	1965	1966	
	RPRM [75,500]	ARP [75,500]	LP [161,350]	A [109,000]	DRV [108,000]	ABV [255,500]	DLP [120,800]	DLV [115,870]	LPRV [311,469]	ARP [745,337]	A [347,450]	DLV [351,870]	Avg [231,470]
						Trawls							
I	–	–	–	–	–	12.1	8.5	–	14.5	16.8	13.1	6.4	11.9
	–	–	–	–	–	(30.9)	(10.3)	–	(45.2)	(125.2)	(45.5)	(19.5)	(46.1)
II	29.0^{b}	21.6^{b}	40.9^{b}	21.5	24.2	13.6	14.5	–	9.4	8.8	8.1	–	19.2
	(21.9)	(16.3)	(66.0)	(23.4)	(26.1)	(34.7)	(17.5)	–	(29.3)	(65.6)	(28.2)	–	(32.9)
III	11.4^{b}	8.5^{b}	16.1	8.7	7.0	6.5	6.5	–	3.1	4.4	–	–	8.0
	(8.6)	(6.4)	(26.0)	(9.5)	(7.6)	(16.6)	(7.9)	–	(9.7)	(32.8)	–	–	(13.9)
IV	3.1	2.3	2.6	2.2	1.7	1.8	2.7	–	2.0	–	–	–	2.3
	(2.3)	(1.7)	(4.2)	(2.4)	(1.8)	(4.6)	(3.3)	–	(6.2)	–	–	–	(3.3)
V	0.2	0.6	0.8	0.3	0.9	0.5	0.7	–	–	–	–	–	0.6
	(0.2)	(0.5)	(1.3)	(0.3)	(1.0)	(1.3)	(0.8)	–	–	–	–	–	(0.8)
						Experimental gillnets							
I	–	–	–	–	–	–	–	–	1.8	3.0	2.6	1.8	2.3
	–	–	–	–	–	–	–	–	(5.6)	(22.4)	(9.0)	(6.3)	(10.8)
II	–	–	47.5^{b}	53.5^{b}	27.3^{b}	15.3	4.4	21.7	27.5	20.3	21.0	–	26.5
	–	–	(76.6)	(58.3)	(29.5)	(39.1)	(5.3)	(25.1)	(85.7)	(151.3)	(73.0)	–	(60.4)

III	147.6[b]	152.7[b]	242.4[b]	272.9	139.2	133.1	81.8	65.9	92.2	81.5	99.1[b]	–	137.1
	(111.4)	(115.3)	(391.1)	(295.7)	(150.3)	(340.1)	(98.8)	(76.4)	(287.2)	(607.4)	(348.6)	–	(256.7)
IV	125.4[b]	129.6[b]	205.8	191.5	134.8	114.7	95.2	53.7	76.5	–	–	–	125.2
	(94.7)	(97.8)	(332.1)	(208.7)	(145.6)	(293.1)	(115.0)	(62.2)	(238.3)	–	–	–	(176.4)
V	59.2	61.2	96.6	56.4	59.5	80.6	50.0	32.4	–	–	–	–	62.0
	(44.7)	(46.2)	(155.9)	(61.5)	(64.3)	(205.9)	(60.4)	(37.5)	–	–	–	–	(84.6)
VI	15.7	14.7	23.7	26.7	27.4	–	–	–	–	–	–	–	21.6
	(11.9)	(11.1)	(38.2)	(29.1)	(29.6)	–	–	–	–	–	–	–	(24.0)
VII	3.7	3.7	10.7	–	–	–	–	–	–	–	–	–	6.0
	(2.8)	(2.8)	(17.3)	–	–	–	–	–	–	–	–	–	(7.6)
						Commercial gillnets							
III	–	–	–	20.4	7.1	–	–	–	–	–	–	–	13.8
	–	–	–	(22.2)	(7.7)	–	–	–	–	–	–	–	(15.0)
IV	–	–	80.9	89.5	28.9	18.4	6.6	21.6	13.5	–	–	–	37.1
	–	–	(130.5)	(97.6)	(31.2)	(47.0)	(8.0)	(25.0)	(42.0)	–	–	–	(54.5)
V	63.3	71.4	135.1	187.2	91.7	58.7	33.1	52.1	30.6[b]	–	–	–	80.4
	(47.8)	(53.9)	(218.0)	(204.0)	(99.0)	(150.0)	(40.0)	(60.4)	(95.3)	–	–	–	(107.6)
VI	62.3	72.8	156.8	185.3	134.3	185.3	–	–	–	–	–	–	132.8
	(47.0)	(55.0)	(253.0)	(202.0)	(145.0)	(473.4)	–	–	–	–	–	–	(195.9)
VII	47.7	53.0	110.3	–	–	–	–	–	–	–	–	–	70.3
	(36.0)	(40.0)	(178.0)	–	–	–	–	–	–	–	–	–	(84.7)
VIII	31.8	29.1	–	–	–	–	–	–	–	–	–	–	30.4
	(24.0)	(22.0)	–	–	–	–	–	–	–	–	–	–	(23.0)

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[a] See Table II for identification of marks.

[b] Estimated by procedure explained in text.

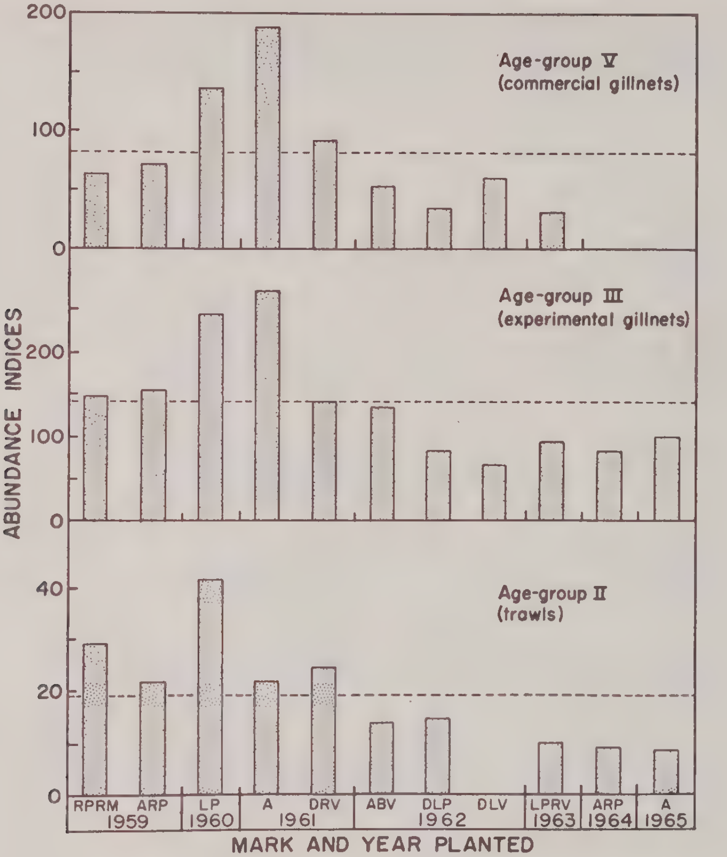

FIG. 3. The relative success of various lake trout plantings based on abundance indices for age-groups II, III, and V taken in three kinds of gear. The dotted horizontal lines represent the average success for all plantings. See Table II for identification of marks.

average size of the fish (8.9–26.5 fish per pound) than in Pycha and King's (1967) studies (2–80 per pound). All the plantings for which they rated success as "poor" consisted of fish which were smaller (34 or more per pound) than any of those considered here. Other factors affecting success of the plantings (e.g., increase in abundance of legal-sized lake trout, changes in the magnitude of the plantings) may have masked the small differences caused by size at release.

Another factor in the success of the plantings may have been differences in planting dates. The fish planted in 1959–62 were all released in May and June (except for the September–October release of 1962), whereas in 1963–66 a large portion of the fish were released under the ice in January–March (Table II). The fish planted in January-March averaged smaller than those planted the following May and June.

The decline in success of the more recent plantings and the failure of continued large-scale releases to raise total abundance of juvenile stocks suggest that the present rate of stocking in the Apostle Islands region may be neither economically sound nor desirable from the standpoint of rehabilitation.

Estimates of the success of hatchery plantings during the first few years after release may have practical application in forecasting returns to the fishery in later years. The average number of age-V lake trout caught per 100,000 ft of commercial gillnets, for example, was 3.79 times the mean number caught per 10 trawl tows at age II. By simple proportion, therefore, the number of fish expected from 100,000 ft of commercial gillnets at age V could be estimated to be 3.79 times the number taken per 10 trawl tows at age II. The dependability of such estimates would of course be affected by the amount of fishing effort and differences in mortality of various plantings between the ages of II and V. Forecasting the availability of lake trout to the fishery could be extremely valuable in the management of a closely controlled fishery.

GROWTH OF HATCHERY-REARED LAKE TROUT

Annual Growth in Length

Annual increments of growth of the hatchery-reared lake trout varied from 1.1 to 5.0 inches (Table VII) after planting in the Apostle Islands region of Lake Superior. The fish averaged 5.8 inches long when planted (age-group I) and were about 25 inches long after 8 years.

Growth was determined from the average lengths at capture of fish of the various age-groups taken in May 1962–66. The first year's growth was completed in the hatchery and was considerably greater than would be expected under natural conditions. This discussion deals only with growth of lake trout after they were released in the lake. The year classes were combined because differences in growth were negligible.

Sources of bias to estimates of growth included gear selectivity, wide ranges in length of the older age-groups, variations in average lengths according to depth of water, and an apparent decrease in length from spring to summer.

Gear selectivity was probably the most severe source of bias. The average lengths of fish of identical age-groups varied widely according to the gear of capture. For example, the average lengths of age-V fish taken in different gears were 12.9 inches for trawls, 15.6 inches for small-mesh gillnets (mean lengths ranged from 14.2 inches in the 2.25-inch mesh nets to 17.2 inches in the 3.5-inch mesh), and 20.1 inches for commercial (4.5-inch mesh) gillnets (Table VII, Fig. 4). The trawls tend to select the smaller members of age-groups above II, experimental gillnets probably select the larger individuals of age-groups II and III and the smaller members of groups VI and VII, and the commercial gillnets select the larger fish of age-groups III–VI and the smaller fish of the VIII group.

TABLE VII. Length distributions of age-groups of hatchery-reared lake trout collected in trawls in May 1962–66 and in small- and large-mesh gillnets in May 1963–66 (year-classes combined). T = trawls; S = small-mesh gillnets; L = large-mesh gillnets.

Total length (*inches*)	I	II		III			IV			V			VI		VII		VIII
	T	T	S	T	S	L	T	S	L	T	S	L	S	L	S	L	L
3.0–3.9	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
4.0–4.9	59	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
5.0–5.9	207	5	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
6.0–6.9	164	110	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–
7.0–7.9	28	465	33	6	2	1	–	–	–	–	–	–	–	–	–	–	–
8.0–8.9	1	428	37	63	5	–	–	–	–	–	–	–	–	–	–	–	–
9.0–9.9	–	110	17	204	94	1	13	4	1	1	1	–	–	–	–	–	–
10.0–10.9	–	16	15	217	301	15	19	21	1	1	4	–	–	–	–	–	–
11.0–11.9	–	–	3	87	224	13	52	140	5	4	8	–	–	–	–	–	–
12.0–12.9	–	–	3	16	79	7	41	229	11	9	38	2	1	–	–	–	–
13.0–13.9	–	1	–	2	35	14	26	192	15	7	78	4	7	–	–	–	–
14.0–14.9	–	–	–	–	20	9	2	152	22	4	126	12	8	3	1	1	–
15.0–15.9	–	–	–	–	6	8	2	83	25	1	114	17	15	3	2	–	–
16.0–16.9	–	–	–	–	1	6	–	40	36	–	80	22	13	5	1	–	–
17.0–17.9	–	–	–	–	–	6	–	14	160	1	48	85	18	21	1	1	–
18.0–18.9	–	–	–	–	–	1	–	5	231	–	30	214	14	45	1	1	–
19.0–19.9	–	–	–	–	–	3	–	1	222	–	20	363	7	134	2	9	1
20.0–20.9	–	–	–	–	–	–	–	1	104	–	7	347	15	203	2	17	3
21.0–21.9	–	–	–	–	–	1	–	1	45	–	10	242	14	227	5	37	2
22.0–22.9	–	–	–	–	–	–	–	–	12	–	9	126	7	185	6	33	9
23.0–23.9	–	–	–	–	–	–	–	–	4	–	–	67	4	130	3	22	5
24.0–24.9	–	–	–	–	–	–	–	–	–	–	–	20	4	63	3	29	6
25.0–25.9	–	–	–	–	–	–	–	–	2	–	–	2	2	33	1	24	13
26.0–26.9	–	–	–	–	–	–	–	–	–	–	–	3	–	21	–	8	4
27.0–27.9	–	–	–	–	–	–	–	–	–	–	–	–	–	7	1	2	4
28.0–28.9	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	2	5
29.0–29.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
30.0–30.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
31.0–31.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
No. of fish	463	1136	113	596	767	85	155	883	896	28	573	1526	129	1082	29	351	54
Avg length	5.8	8.0	8.7	10.1	11.1	13.6	11.8	13.4	18.6	12.9	15.6	20.1	18.5	21.7	21.3	22.9	24.9

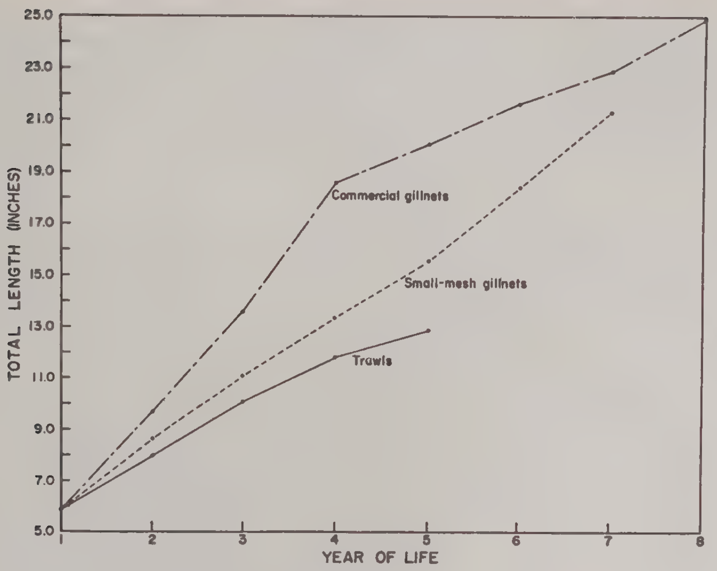

FIG. 4. Average lengths at capture of hatchery-reared lake trout of different ages, taken in three kinds of gear.

Estimates of growth were further complicated by the wide range in length of the older age-groups. The range in length of age-I fish when planted (Table VIII) was only 4.7 inches (from 3.9 to 8.6 inches), but at age V the ranges

TABLE VIII. Average total lengths (inches) of various age-groups of hatchery-reared lake trout from trawls fished at different depths in the Apostle Islands region, June 1962–63. Number of fish in parentheses.

Date of collection and depth (*fath*)	Age-group and fin mark[a]					
	I	II	II	III	III	IV
June 1962	ABV	A	DRV	LP		
15–19	–	8.0	7.8	11.7	–	–
	–	(12)	(5)	(5)	–	–
20–29	6.2	7.6	7.8	10.1	–	–
	(27)	(97)	(76)	(90)	–	–
30–34	6.2	7.9	7.7	9.8	–	–
	(8)	(16)	(31)	(17)	–	–
June 1963	LPRV	ABV		A	DRV	LP
15–19	5.7	7.9	–	11.6	10.6	12.4
	(10)	(8)	–	(15)	(6)	(9)
20–29	5.9	8.0	–	10.5	9.9	11.8
	(40)	(275)	–	(110)	(62)	(60)

[a]See Table II for identification of marks.

widened considerably and varied according to the type of gear in which they were captured. Age-group V fish were from 9.9 to 17.6 inches long in trawls, from 9.9 to 22.7 inches in small-mesh gillnets, and from 12.0 to 26.9 inches in commercial gillnets. The length range of age-group V lake trout, therefore, was 17.0 inches (from 9.9 to 26.9 inches).

The average lengths of hatchery-reared lake trout varied also according to depth of water. Records of lake trout from trawls fished in June 1962–63 by the *Siscowet* in the Apostle Islands region indicated that the average lengths of fish of age-groups I and II did not decrease with depth but that fish of age-groups III and IV were without exception larger in shallow water (Table VIII). Records from experimental gillnets (not given here) indicated that the average lengths of fish of age-groups II–V decreased with depth of water during all seasons. An inverse relation between depth of capture and average length of lake trout (all age-groups combined) was demonstrated by catches of the R/V *Kaho* in Keweenaw Bay, Lake Superior, in 1964–65 (Table IX). Mean length decreased steadily with increasing depth of water. Fish from depths of less than 10 fath averaged 7–10 inches longer than those from depths greater than 39 fath.

TABLE IX. Average total lengths (inches) of lake trout taken in trawls by the R/V *Kaho* from various depths in Keweenaw Bay, Lake Superior, 1964–65. Numbers of fish in parentheses.

Depth (*fath*)	1964 Spring	1964 Fall	1965 Spring	1965 Fall	Samples combined[a]
<10	17.1	20.5	18.9	–	18.8
	(20)	(5)	(12)	–	(37)
10–19	14.8	18.3	20.4	16.5	17.5
	(19)	(12)	(20)	(17)	(68)
20–29	11.8	17.3	19.3	15.7	16.0
	(138)	(22)	(43)	(51)	(254)
30–39	8.7	11.5	12.5	10.4	10.8
	(407)	(89)	(190)	(134)	(820)
>39	9.1	10.5	11.7	–	10.4
	(76)	(87)	(37)	–	(200)

[a] Unweighted mean.

The presence of larger lake trout in shallow water may be due to changes in food preferences with increased size of fish. Dryer et al. (1965) found that the importance of fish in the diet of lake trout increased as the lake trout grew larger. As the larger members of an age-group become more dependent on fish for food they may migrate to shallow water, where small forage species (mainly American smelt, *Osmerus mordax*) are more abundant. Fish of age-groups I and II and the smaller members of age-groups III–V depend mostly on crustaceans for food and may therefore remain in deeper water (Dryer, 1966).

The average lengths of fish of certain age-groups taken from the same depth with the same gear decreased from spring to summer. Almost without exception the average lengths of lake trout of age-groups III–V from small-mesh gillnets fished at 21–26 fath were shorter in July than in May of the same year (Table X).

TABLE X. Average lengths (inches) of lake trout from small-mesh gillnets fished at depths of 21–26 fath in May and July 1963–66. Number of fish in parentheses.

Year and month of capture	Year-class, fin mark,[a] and age-group								
	1959	1960		1961			1962	1963	1964
	LP	DRV	A	ABV	DLP	DLV	LPRV	ARP	A
1963	IV	III	III	II					
May	13.7	11.5	12.2	8.4	–	–	–	–	–
	(27)	(6)	(18)	(2)	–	–	–	–	–
July	13.3	11.3	11.8	9.5	–	–	–	–	–
	(102)	(55)	(104)	(9)	–	–	–	–	–
1964	V	IV	IV	III	III	III	II	–	–
May	15.7	13.6	14.1	11.0	10.5	11.5	9.2	–	–
	(159)	(132)	(236)	(225)	(55)	(69)	(21)	–	–
July	13.8	12.4	13.2	11.0	10.4	11.1	9.1	–	–
	(31)	(47)	(44)	(225)	(61)	(25)	(51)	–	–
1965	VI	V	V	IV	IV	IV	III	II	–
May	18.3	15.6	16.6	13.0	12.7	13.2	11.2	8.2	–
	(42)	(55)	(57)	(189)	(63)	(50)	(133)	(53)	–
July	19.3	14.8	14.6	12.9	12.2	12.6	11.1	8.7	–
	(8)	(26)	(23)	(142)	(67)	(25)	(159)	(89)	–
1966	VII	VI	VI	V	V	V	IV	III	II
May	20.3	18.2	19.0	15.1	14.5	16.0	13.2	11.0	9.0
	(21)	(29)	(36)	(202)	(57)	(32)	(186)	(261)	(33)
July	24.7	17.9	19.6	14.2	13.5	13.9	12.6	10.9	9.1
	(4)	(8)	(5)	(66)	(27)	(16)	(135)	(411)	(40)

[a] See Table II for identification of marks.

The length distributions of age-IV and age-V lake trout taken in May and July (Table XI) give evidence that the larger members of an age-group were poorly represented on the fishing grounds in July. The percentage of age-V lake trout longer than 15.4 inches dropped from 37.1% in May to 12.1% in July; age-IV, from 6.5% in May to nil in July.

TABLE XI. Length distributions of two age-groups of lake trout from small-mesh gillnets fished at 24–26 fath in May and July 1966.

Total length (*inches*)	Age-group, fin mark,[a] and month of collection			
	IV — LPRV		V — ABV	
	May	July	May	July
9.5–9.9	–	1	–	–
10.0–10.4	–	1	1	–
10.5–10.9	2	5	1	1
11.0–11.4	11	6	1	–
11.5–11.9	22	17	1	2
12.0–12.4	28	31	5	3
12.5–12.9	30	34	8	3
13.0–13.4	28	16	14	9
13.5–13.9	18	10	24	9
14.0–14.4	12	10	33	9
14.5–14.9	14	3	21	8
15.0–15.4	9	1	18	14
15.5–15.9	6	–	21	4
16.0–16.4	1	–	15	3
16.5–16.9	3	–	11	–
17.0–17.4	1	–	4	1
17.5–17.9	1	–	7	–
18.0–18.4	–	–	4	–
18.5–18.9	–	–	2	–
19.0–19.4	–	–	4	–
19.5–19.9	–	–	3	–
20.0–20.4	–	–	–	–
20.5–20.9	–	–	2	–
21.0–21.4	–	–	2	–
Total	186	135	202	66
Avg length	13.2	12.6	15.1	14.2
Percentage over 15.4 inches	6.5	0.0	37.1	12.1

[a] See Table II for identification of marks.

The apparent decrease in length from spring to summer, like the decrease in length with increasing water depth mentioned above, may be due to changes in food preferences. The larger members of an age-group may migrate to shallow water some time after May in search of small forage fish. Dryer (1966) found some evidence that lake trout moved from deep to shallow water from spring to fall.

Because of the wide variation in average lengths of fish of identical age-groups from the various gears (Table VII, Fig. 4) and because the catches from trawls and gillnets cannot be combined on the basis of common units of effort, sound estimates of general growth are impossible. Annual increments of growth of lake trout from trawls decreased from 2.2 inches in the 2nd year of life to 1.1 inches in the 5th. The fish were 12.9 inches long at the end of 5 years. Lake trout from small-mesh gillnets grew 2.9 inches in their 2nd year of life, 2.9 in their 6th, and 2.8 inches in their 7th. The fish were 21.3 inches long at the end of 7 years. The annual increments of fish from commercial gillnets ranged from 5.0 inches in the 4th year to 1.2 inches in the 7th year of life. The fish were 24.9 inches long at the end of 8 years.

Native lake trout collected in trawls and small-mesh gillnets from Lake Superior in 1952–53 grew 3.9 inches in the 1st year of life (compared with 5.8 inches for hatchery-reared fish), were 6.7 inches long at the end of the 2nd year, and reached 8.6 inches after 3 years (Eschmeyer, 1956). The 2nd- and 3rd-year increments were 2.8 and 1.9 inches, respectively, compared with 2.2 and 2.1 inches for hatchery-reared lake trout from trawls in the Apostle Islands region in the present study.

Seasonal Growth

Seasonal growth of hatchery-reared lake trout was determined from the average lengths of fish from the 1962-ABV planting during various time periods in 1962–66. This was the only group for which complete records were available for ages I through V.

The records from trawls suggest that the fish grew at a nearly uniform rate during their 2nd and 3rd years of life (Fig. 5). The average length of the age-I fish (2nd year of life) in early June was the same (5.8 inches) as

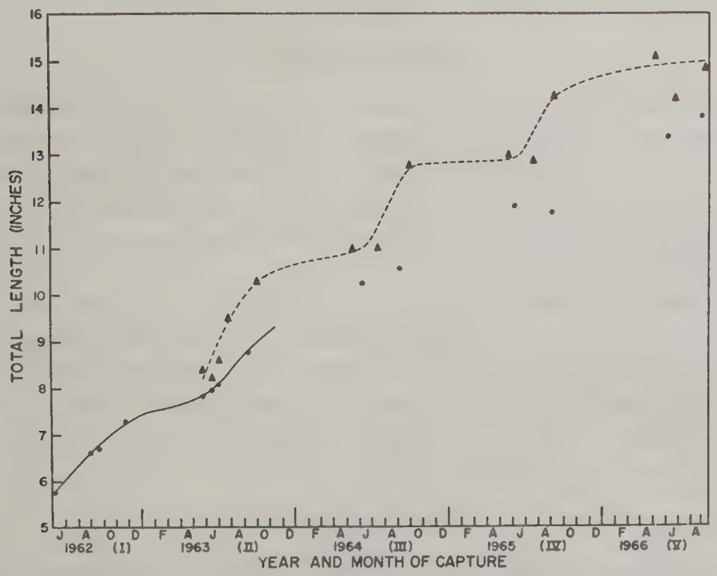

Fig. 5. Average lengths of lake trout recaptured from the 1962-ABV planting in trawls (circles) and experimental gillnets (triangles) for various dates, 1962–66. The age-groups are in parentheses after the year of capture. The curves were drawn by inspection.

that of the fish planted in May. The fish had grown 0.8 inch by early September and 1.5 inches by the end of November.

Late fall or winter growth was evidenced by the increase in average length from 7.3 inches in late November 1962 to 7.8 inches the following May. Third-year growth of lake trout from trawls was 2.3 inches (from June 1963 to June 1964). Over 65% of the growth (1.5 inches) took place after mid-September 1963. The curve for fish from trawls (Fig. 5) was not extended beyond the 3rd year of life because samples were collected only in June and September in the later years.

Lake trout from small-mesh gillnets appeared to grow rapidly in late summer and fall (Fig. 5). Fourth- and 5th-year growth did not begin before August but by late September the fish had grown well over 1 inch. The 5th-year growth (from May 1965 to May 1966) was 2.1 inches, of which 0.8 inch (38%) took place after September,

The apparent difference in seasonal growth of lake trout from trawls and small-mesh gillnets may be influenced by the migration in early summer of larger members of an age-group to shallow water. If the larger fish left the vicinity of the index stations in early summer or throughout the summer, estimates of growth based on the average lengths of the remaining smaller fish are not representative of the total population.

Eschmeyer (1956) suggested that lake trout of ages 0 and I in Lake Superior continue to grow to or beyond the end of the calendar year. Rahrer (1967) found that lake trout of ages I and II in Lake Superior had completed only 63% of their annual growth by October and fewer than 30% of ages VII–XII had started growing by October.

FUTURE PROSPECTS

The remarkable recovery of lake trout stocks in the Apostle Islands region makes the outlook for complete success of lake trout rehabilitation appear excellent. Natural reproduction, which has already been demonstrated, should soon replace hatchery plantings. The percentage of hatchery fish among juvenile stocks began to decline in 1966 and the trend should continue with the buildup of native stocks.

The decline in the success of hatchery plantings since 1961 and the failure of juvenile lake trout to increase in abundance since 1962 suggest that the present rate of stocking may be larger than is necessary to maintain optimum abundance. Hatchery-reared lake trout in excess of those needed in the Apostle Islands region might well be diverted to other areas where the progress of rehabilitation has been slow.

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SALT WATER RADIOECOLOGY—

A fresh approach for studying the relationships between marine animals, plants, and their environment.

by **Dr. Thomas W. Duke**
Assistant Director, Radiobiological Laboratory

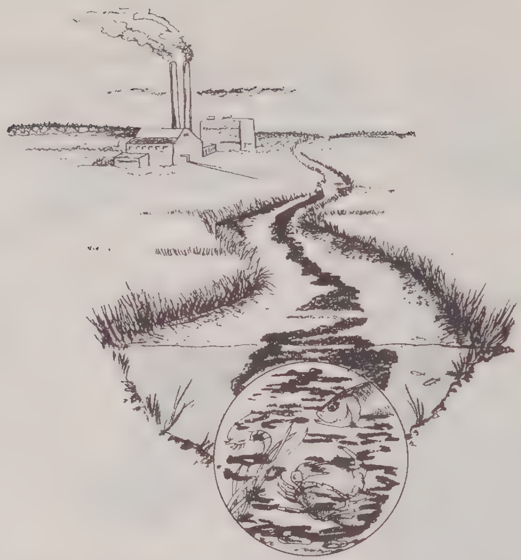
Here, a simulated marine habitat is checked with a sensitive instrument to determine extent of radioactivity after the addition of radioactive zinc. Both plants and animals are checked.

RADIOECOLOGY is a relatively new term that describes the study of radioactivity in our environment and the use of radioactive elements in ecological studies. The term is composed of two words —"radio" which here refers to radioactivity and "ecology" which is derived from the Greek *Oikos*, meaning "house" or "place to live." Ecology has been defined as the study of animals and plants "at home" and as "the science of the living environment." Although the term radioecology was coined just recently (in the 1950's) radioactivity has been present in man's environment since the earth was formed and references to principles that were ecological in nature appeared in writings of the early philosophers. The need for this "new" division of ecology, however, was brought about by technological advances of modern man.

Man has added much radioactivity to his environment by exploding nuclear weapons in the atmosphere and by releasing wastes containing radioactive materials into rivers and coastal waters. It was not until 1945 that man-made radioactivity began to appear in the oceans. At this time the world "fallout," that is, radioactive particles that settle to the surface of the earth after nuclear explosions, came into use. About 61 percent of these radioactive materials fall into the ocean in our hemisphere (approximately 61 percent of the earth's surface in the Northern Hemisphere is covered with water) and some of the fallout on land is leached from the soil and carried by rivers to estuaries and the oceans. The major source of radioactivity in the marine environment, however, is from nuclear fuel processing and production plants, and from other industries which discharge wastes into coastal waters or into rivers emptying into the sea. For example, the Hanford Atomic Production Plant in the state of Washington releases radioactivity directly into the Columbia River and much of the radioactivity is carried to the Pacific Ocean 350 miles downstream. These and other radioactive materials released into the marine environment by man are a potential health hazard because the radioactivity can be returned to him through seafood products.

RADIOACTIVE elements act essentially the same as their nonradioactive counterparts when released into the marine environment. For example, radioactive zinc (zinc 65), has been shown to follow the same pathways as stable zinc in the marine environment. Therefore, if radioactive elements are present in sea water, they will be accumulated by organisms living in the sea just as the stable elements are. Organisms become radioactive in different ways: some (plants) accumulate radioactivity directly from water, some (clams and oysters) by feeding on suspended material that contains radioactivity, and some (large fish) by feeding on other animals that are radioactive. Radioactivity thus is passed up the food chain to man through a series of organisms that are eating and being eaten. Although studies of the manner in which radioactivity is accumulated and lost by marine animals and plants is an important aspect of radioecology, another, just as important, is the use of radioactive elements to study the complex relationships that exist among animals, plants, and their environment.

Many new research possibilities have arisen in the field of ecology as radioactive tracers have become available. Instruments that measure radioactivity are now highly sensitive and this advance has made possible the application of radioactive tracers to problems beyond the range of standard



Much of the radioactive material introduced into our marine habitats comes from nuclear fuel processing and production plants and other industries located on coastal streams.

methods. For example, marine biologists are often interested in the primary productivity—the amount of carbon fixed by photosynthesis in plants—of a particular area. In many oceanic areas this production is small and difficult to measure. The production of radioactive elements gave us a new, more sensitive method for measurement of primary productivity with radioactive carbon (carbon 14). Radioactive elements have become particularly useful in other studies which include the movement of elements in the environment, food and feeding of marine animals, and tagging of marine organisms and sediments so that their movement can be followed.

Marine scientists at university, state, and federal laboratories in North Carolina are actively participating in radioecological studies. As much (possibly more) of this type of research is in progress in North Carolina as in any part of the country. Scientists working on similar problems in the different institutions exchange information freely so that a spirit of cooperation exists. The research at one of these laboratories and its cooperative arrangement with a state university are described here.

THE Radiobiological Laboratory on Pivers Island, near Beaufort, North Carolina, has a staff of 24 which includes 11 biologists who, under the leadership of Dr. T. R. Rice, Laboratory Director, are engaged in some aspect of radioecological research. This federal laboratory is supported jointly by the Bureau of Commercial Fisheries and the Atomic Energy Commission. The purpose of research at the laboratory is twofold: (1) to determine the fate of radioactive elements that are released into the estuarine environment and the effect of this radioactivity on estuarine plants and animals, and (2) to develop and apply radioisotopic methods to studies of estuarine ecology. As part of this work, the staff has been assigned the responsibility for evaluating the possible radiological effects of the construction and operation of nuclear reactors on fishery resources.

The fate of radioactive elements released into the estuarine environment from nuclear reactors or other sources depends upon the route they take in the estuary. Radioactive materials can remain in solution in the water (much as salt in sea water) or settle to the bottom. Plants and animals may accumulate the radioactive elements either from the water or sediment. If accumulated by seafood organisms, the radioactivity could adversely affect the organisms and also could be passed on to man. Biologists at the Radiobiological Laboratory are studying this accumulation and its effects through experimentation in the laboratory and in the field.

In the laboratory, the staff observes plants and animals in various types of aquaria and ponds filled with radioactive sea water, and measures the simultaneous uptake of radioactivity by a number of different species. Fishes such as the croaker, spot, flounder, sea mullet, and menhaden; crustaceans, such as the shrimp and the blue crab; and molluscs, such as the oyster, clam, and scallop have been exposed to radioactive materials and later checked for their accumulation of radioactivity. The radioactive content of the organisms is determined with specialized electronic equipment—multichannel analyzers. These experiments usually involve placing a plant or animal or communities of organisms in tanks containing sea water with a known amount of the radioactive substance. In some experiments, the water does not contain radioactive elements but the organisms are fed radioactive food.

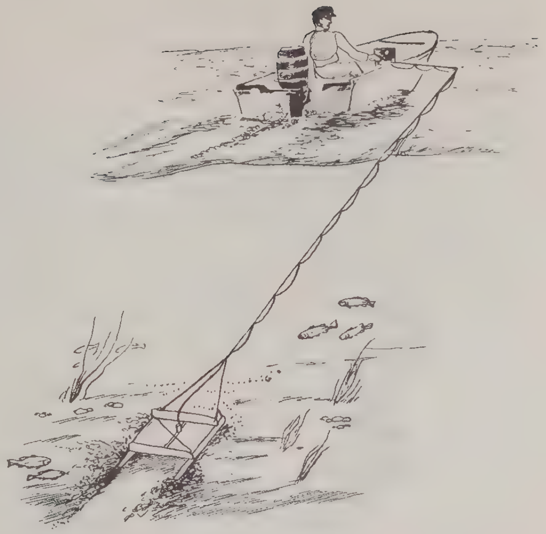
The results of these experiments have been enlightening. For instance, the accumulation of materials with a "half-life" long enough to reach man (the "half-life" is the amount of time required for a radioactive material to lose one-half of its radioactivity by natural decay) is for the most part confined to the bones, scales, shells, and viscera of fish and shellfish; these parts are not normally eaten. Exceptions, of course, are the clams and oysters, which are eaten with viscera intact, and sardines, which are eaten with both bones and viscera.

Experiments are conducted in the laboratory also to determine the changes that might occur in the body chemistry or bodily shapes of plants and animals subjected to radioactivity. Much of this study has been with the blood of fishes, for it is believed that any radiation-induced physiological changes will occur first in the blood. Other studies are concerned with what might happen to a population of fish exposed to radioactivity. Although the study is not yet complete, the chance seems to be small that fish would be adversely affected from exposure to levels of radiation that would not affect man. The animals used thus far in testing have been found to be resistant to greater levels of exposure than those man is capable of withstanding.

Most of the experiments described have been studies of animals held in the laboratory, apart from the rest of the marine community. To understand how radioactive materials move through the community, experiments ideally should be conducted in the natural environment, such as a sound or bay. For obvious reasons, however, the natural environment cannot be made radioactive for such a study. To avoid contaminating the environment, experiments are conducted in a very large outdoor pond in which a marine habitat is simulated. A large number of plants and animals have been placed in a 40- by 60-foot salt-water pond walled with concrete and allowed to live much as they would in a shallow estuary. Several kinds of fishes, crabs, and marsh grasses, along with oysters, clams, and snails, have been placed together in water made radioactive by the addition of radioactive zinc. It has been found that sediments, which were usually missing in the laboratory experiments, play a large role in the distribution of this radioactive element.

RADIOACTIVE elements are used as tracers at the laboratory to study many aspects of estuarine ecology. These tracers are particularly valuable in obtaining answers to some of the problems of food and feeding habits of oysters and clams and determining the best location for oyster beds. Before radioactive elements became available, it was very difficult and time consuming to compare the suitability of different kinds of phytoplankton (minute plants that float in water) as food for oysters and clams. Some of the plants consumed by these animals are used for nutrition and others are quickly discarded without being used. To test the nutritive value of different types of phytoplankton, cells are labeled with radioactive elements and then fed to the oysters and clams. After several hours the animals are dissected and the muscles that control the opening and closing of the shell are removed and analyzed for radiactivity content. If radioactivity from the labelled cells appears in the muscle, the phytoplankton presumably was used for nutrition by the animal.

In the natural environment these animals must have sufficient food and must be located in an area that is not subject to excessive "silting in." Radioactive material that is attached to fine particles of sediment can be used to determine the most favorable location for shellfish beds in respect to the silt. The labeled sediment is released into the water near the area of the proposed bed and is deposited just as natural particles in the water. A sled-like vehicle containing an electronic device that can detect radioactivity is then pulled across the bottom sediment. The appearance of radioactivity in the bottom sediment indicates where the labeled particles settled and thus where silting will take place. Also, the time required for the radioactive particles to reach the bottom indicates the rate at which silting will occur.



In order to monitor the sediment deposits, a "sled" containing radioactivity-detecting equipment is pulled along the ocean or estuary bottoms. The device can be operated by one man.

Both the Bureau of Commercial Fisheries and the Atomic Energy Commission desire to stimulate the interest of students in marine biology and to contribute to their training; therefore a close affiliation was established between the laboratory and the Zoology Department at North Carolina State University at Raleigh, North Carolina—five staff members of the laboratory have been appointed Adjunct Professors. Several graduate students from the Zoology Department are fulfilling their requirements for research at the Radiobiological Laboratory. One or more of the staff members holding adjunct appointments supervise a student's research and coordinate his activities in cooperation with faculty members on campus. Projects undertaken by students include studies of the role of marsh grass in the dynamics of the esturaine ecosystem, observations on the contribution of "high" and "low" marsh areas to nutrient cycles in the estuary, and investigations of the capacity of clams and shrimp to use decaying marsh grass and other nonliving material for nourishment. This cooperative arrangement between the laboratory and university is of mutual benefit; it increases university teaching facilities, both of staff and technical equipment, and provides information exchange between the laboratory staff and the students and faculty of the university. Also, the arrangement gives students an opportunity to use specialized equipment that is not always available in marine laboratories and to participate in "on-the-job" research training.

The importance of studies in the field of radioecology increases as the levels of radioactivity in our environment increase and as we find additional uses for radioactive elements in ecological research. It is to be hoped that future scientists can concentrate on applying the use of radioactive elements to such tasks as eradicating predators and parasites of fish and shellfish. Whatever the emphasis, much of the research will no doubt take place in North Carolina. ◆

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pp. 541–545

A Technique for Studying the Exchange of Trace Elements Between Estuarine Sediments and Water[1]

Trace elements are continuously exchanged between sediments and water in the estuarine environment. This exchange is an important part of the biogeochemical cycling of these elements and often determines their availability to the biota. Sediments usually contain large concentrations of trace elements relative to the water and serve as a reservoir for the elements. Radioisotopes have been used experimentally to study the sediment–water exchange of phosphate (Pomeroy, Smith, and Grant 1965), zinc (O'Connor and Renn 1964; Johnson, Cutshall, and Osterberg 1966; Bachmann 1963; Sonnen 1965), and other elements (Carritt and Goodgal 1954).

In this paper we describe a technique and specialized equipment for studying the exchange of elements between sediments and water. Exchange rates of zinc are determined for a series of sediment samples from the Newport River estuary at Beaufort, North Carolina.

MATERIALS AND METHODS

Natural cores of estuarine sediments are collected with a coring device constructed with a polyethylene cylinder that is plugged with a vinyl stopper and detached after a core is taken (Fig. 1). The cylinders are then transported to the laboratory and submerged in water from the sampling station in a 30-gallon (0.11 m^3) plastic container. The water, circulated by aeration, is maintained at 22 ± 2C and the *p*H and salinity are recorded. The sediment is left in contact with the water until the concentration of the trace element of interest becomes constant in the water. In the present experiments, zinc was analyzed periodically as reported by Duke, Willis, and Price (1966) until the difference between two consecutive measurements was less than 5% of the total concentration.

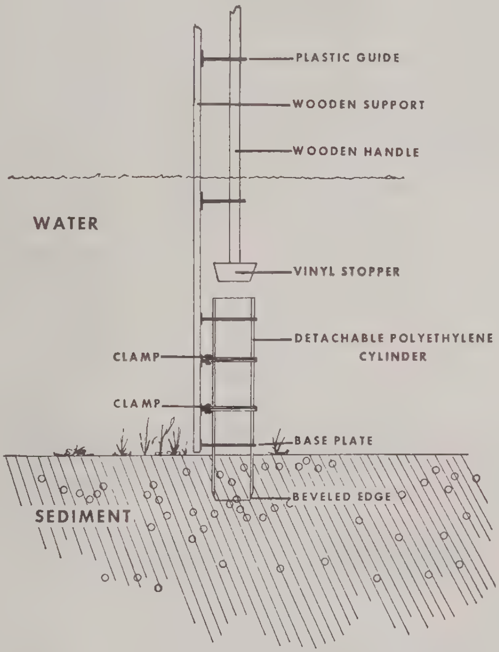

Fig. 1. Corer for taking sample of sediment and overlying water.

After this equilibrium is reached, the cylinders containing the cores and about 800 ml of water are removed from the plastic can. The water is pumped from the cylinder and filtered through a 0.45-μ membrane filter. The inside of the cylinder is wiped clean, about 600 ml of the filtered water are returned to the cylinder, and the remainder is used for chemical analysis. These operations must be completed carefully to avoid disturbance of the sediment surface.

After the filtered water is in place over the core, the cylinders are slipped into a specially constructed lead shield (Fig. 2). The shield consists of three parts arranged so that a 2-inch (5.4 cm) sodium iodide crystal detects only the radiation passing through a narrow slit (1.6 cm high) focused on a limited portion of the sample cylinder. The detector is hooked to a rate meter and 10-mv recorder. The radioactivity from a

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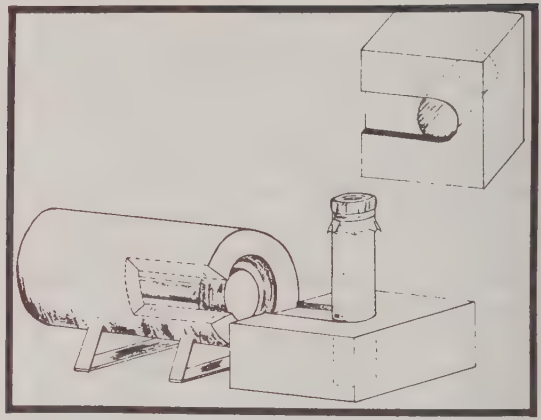
[1] This research was supported through a cooperative agreement between the U.S. Fish and Wildlife Service and the U.S. Atomic Energy Commission.



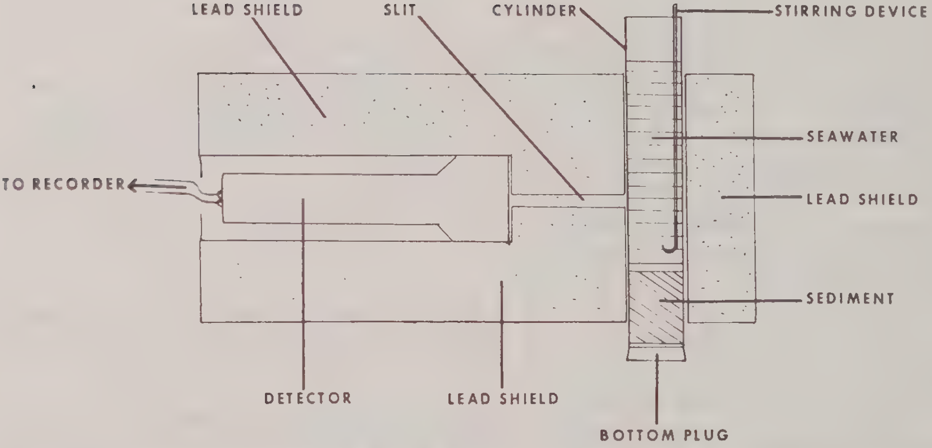


Fig. 2. Apparatus for measuring loss of radionuclide from water to sediment instantaneously and continuously.

narrow wedge of the water column can thus be measured and recorded both instantaneously and continuously.

Carrier-free radioactive tracer is added to the column of water through a plastic pipette positioned so that the tracer is released 8 cm below the surface and in the center of the water column. A J-shaped plastic aeration tube is attached to the inside wall of the cylinder and extends to the midpoint of the water column. Filtered compressed air is pumped through the tube at a rate that does not disturb the sediment surface but does ensure circulation and mixing of water above the sediment. Preliminary studies showed that when the cylinder is in position, radiation from the sediment cannot be detected. Thus, only loss of the tracer from the water is recorded. A blank cylinder containing only filtered water is spiked with tracer and analyzed so that a curve representing movement of the tracer due to processes other than exchange with the sediment can be determined. During the analysis, the top of the cylinder is covered with Saran Wrap to ensure that radioactivity is not lost in the spray from bursting air bubbles.

In the exchange of any element between water and sediments, at equilibrium, when the concentration of the traced element in the water remains constant, the rate of movement of the element from water to sediment equals the rate of movement from sediment to water. Thus

$$\begin{aligned} \rho w \to s &= \rho s \to w \\ &= \rho \text{ (the overall rate of exchange).} \end{aligned}$$

Or written in the notation of compartmental analysis (Sheppard 1962), for the general case of n water compartments and m sediment compartments

$$\begin{aligned} &(\rho w_1 \to s_1 + \rho w_1 \to s_2 \ldots + \rho w_1 \to s_m) \\ &+ (\rho w_2 \to s_1 + \rho w_2 \to s_2 \ldots + \rho w_2 \to s_m) \\ &\quad \cdot \quad \cdot \quad \cdot \\ &+ (\rho w_n \to s_1 + \rho w_n \to s_2 \ldots + \rho w_n \to s_m) \\ &\quad = (\rho s_1 \to w_1 + \rho s_1 \to w_2 \ldots + \rho s_1 \to w_n) \\ &\qquad + (\rho s_2 \to w_1 + \rho s_2 \to w_2 \ldots + \rho s_2 \to w_n) \\ &\qquad\quad \cdot \quad \cdot \quad \cdot \\ &\qquad + (\rho s_m \to w_1 + \rho s_m \to w_2 \ldots + \rho s_m \to w_n), \end{aligned}$$

where $\rho 1 \to 2$ = rate of movement of traced substance from compartment 1 to compartment 2; w = water; s = sediment; and t = time. In later equations (below), S_1 = amount of traced substance in compartment 1; R_1 = absolute amount of tracer in compartment 1; and a_1 = specific activity of compartment 1. If a tracer is introduced into the water, its movement from the water can be described:

$$\begin{aligned} dR_w/dt = &-\text{rate of movement of tracer} \\ &\quad \text{from water to sediment} \\ &+\text{rate of return of tracer} \\ &\quad \text{from sediment to water.} \end{aligned}$$

At any instant the rate of movement of tracer from water to sediment equals the rate of movement of traced substance from water to sediment times the fraction labeled = $\rho \times a_w$, and similarly the rate of movement of tracer from sediment to water = $\rho \times a_s$, or $dR_w/dt = -\rho \times a_w + \rho \times a_s$. Since many compartments may be present in the sediment

$$\begin{aligned} dR_w/dt = -[&(\rho w_1 \to s_1 \times a_{w_1} + \rho w_1 \to s_2 \times a_{w_1} \\ &\quad \ldots + \rho w_1 \to s_m \times a_{w_1}) \\ &+ (\rho w_2 \to s_1 \times a_{w_2} + \rho w_2 \to s_2 \times a_{w_2} \\ &\quad \ldots + \rho w_2 \to s_m \times a_{w_2}) \ldots \\ &+ (\rho w_n \to s_1 \times a_{w_n} + \rho w_n \to s_2 \times a_{w_n} \\ &\quad \ldots + \rho w_n \to s_m \times a_{w_n})] \\ + [&(\rho s_1 \to w_1 \times a_{s_1} + \rho s_1 \to w_2 \times a_{s_1} \\ &\quad \ldots + \rho s_1 \to w_n \times a_{s_1}) \\ &+ (\rho s_2 \to w_1 \times a_{s_2} + \rho s_2 \to w_2 \times a_{s_2} \\ &\quad \ldots + \rho s_2 \to w_n \times a_{s_2}) \ldots \\ &+ (\rho s_m \to w_1 \times a_{s_m} + \rho s_m \to w_2 \times a_{s_m} \\ &\quad \ldots + \rho s_m \to w_n \times a_{s_m})]. \end{aligned}$$

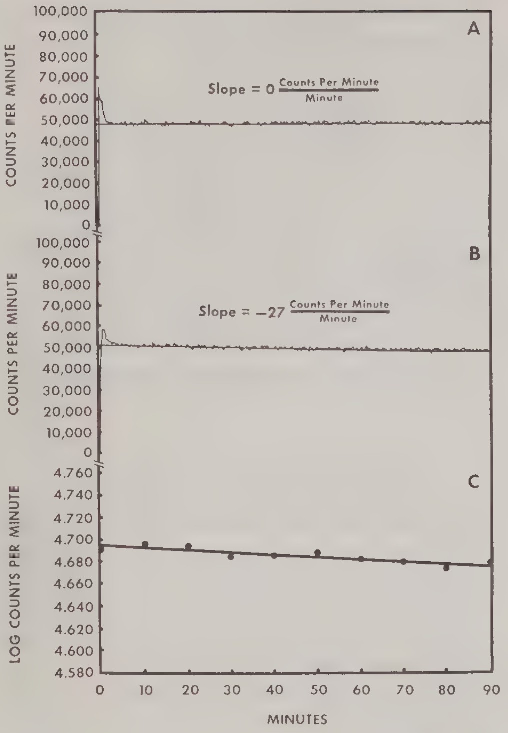


Fig. 3. Rates of movement of ^{65}Zn from water to sediments and walls of plastic cylinders. Graph A represents movement of ^{65}Zn in control cylinder; B represents movement of ^{65}Zn from water to sediment in typical sample from Newport River, North Carolina; and C shows a plot of log concentration of ^{65}Zn in the water vs. time to be a straight line for first 90 min.

However, for determining the overall exchange rate across the sediment–water interface, it should be possible to describe the water–sediment exchange system by equations for only two exchanging compartments, water and sediment, during a short interval after the introduction of tracer (principle of lumping), giving:

$$dR_w/dt \cong \rho \times (a_s - a_w),$$

and near $t = 0$, $a_s \cong 0$. Therefore,

$$dR_w/dt \cong -\rho \times a_w ,$$

and since

$$a_w = R_w/S_w ,$$

$$dR_w/dt \cong -\rho \times R_w/S_w ,$$

and

$$dR_w/R_w \cong -(\rho/S_w)\, dt .$$

Assuming ρ and S_w constant and integrating over limits $R = R_{w_0}$, $t = 0$ to $R = R_w$, $t = t$, then

$$\ln R_w \cong \ln R_{w_0} - (\rho/S_w)\, t ,$$

$$2.303 \log R_w \cong 2.303 \log R_{w_0} - (\rho/S_w) t ,$$

and

$$\log R_w \cong \log R_{w_0} - (\rho/2.303 S_w) t .$$

Therefore, lumping of the water and sediment compartments into only two compartments and assuming that $a_s = 0$ is permissible, as long as a plot of $\log R_w$ vs. t gives a straight line. This is shown to be true for the first 90 min in Fig. 3.

Now since $dR_w/dt \cong -\rho \times a_w$ during the first 90 min, then, near $t = 0$,

$$\rho = -\frac{dR_w/dt}{a_w} .$$

The rate, dR_w/dt is assumed to be equal to the slope of the R_w vs. t plot which is calculated by inspection from the first 35 min of the curve after the elimination of the first 5 min during which mixing occurred. This assumption is permissible since the slope is essentially constant over the first 35 min after the addition of tracer (Fig. 3). The rate of exchange, ρ, is then computed from the values of dR_w/dt and that calculated for a_w at $t = 0$.

ρ is the rate of exchange of the substance between the water and sediment actually contained in the experimental cylinders. To make this rate applicable to the estuary, the rate is divided by the exposed surface area of the sediment contained in the cylinder, giving

$$\frac{\rho w \rightleftarrows s}{m^2} = -\frac{dR_w/dt}{a_w \text{ (surface area of sediment)}} .$$

The exchangeable amount of element in the sediment can be determined from the specific activity in the water after the tracer has equilibrated with the sediments. After the cylinders are analyzed for 2 hr for the loss of the tracer, they can be removed from the shield, stored with aerating device in place, then periodically replaced in the shield and analyzed for tracer content. At equilibrium, that is, when there is no further loss of isotope from the water, the amount of exchangeable element in the sediment can be calculated from the expressions:

Specific activity of water = Specific activity of sediment;

$$R_w/S_w = R_s/S_s ;$$

$$S_s = R_s S_w / R_w .$$

APPLICATION OF TECHNIQUE

Cores collected in June 1967 from the mouth of the Newport River estuary in Beaufort, N.C., were analyzed for rate of zinc exchange by this technique. Cores consisted of 32% sand (>0.05 mm), 38% coarser silt (0.05–0.025 mm), 18% coarse silt (0.025–0.005 mm), 2% fine silt (0.005–0.002 mm), and 10% total clay (<0.002 mm). Carrier-free ^{65}Zn as ^{65}ZnCl$_2$ was used as the tracer. Exchange rates were calculated as described above, assuming that the tracer mixed immediately and completely with the exchangeable zinc in the water and that the stable zinc concentration in the water was constant during the 30-min period in which loss of the tracer was observed. The average rate of exchange for 10 cores was 17 ± 4 μg of Zn hr^{-1} m^{-2}. This technique is applicable to studies of any other element with a convenient gamma-emitting isotope, as long as no isotopic effects occur.

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Tattoo-Marking of Fingerling Salmonids with Fluorescent Pigments

Tattooing is a useful method for marking fish because a number of different marks may be made by combinations of color, number, and location (Dunstan and Bostick, 1956). Nonfluorescent-pigment tattoos have been retained up to 5 months (Chapman, 1957). Although 5 months is sufficient for many experiments, a longer-lasting pigment would extend the usefulness of the method.

Fluorescent pigments for tattoo-marking of fingerling salmonids were first used in studies of fish mortality in turbines at Shasta Dam.[1] These pigments were first considered by the U.S. Bureau of Commercial Fisheries because of the need for more marks consisting of single tattoos in a standard location on the fish. Marks that require multiple tattoos and multiple locations are more time consuming and susceptible to error. Because fluorescent and nonfluorescent pigments of the same color can be readily differentiated under ultraviolet (UV) light, the number of usable pigments could be doubled by using both types of pigments.

Since 1963, over 100,000 coho salmon (*Oncorhynchus kisutch*), chinook salmon (*O. tshawytscha*), and rainbow trout (*Salmo gairdneri*) have been tattooed with fluorescent pigments by the Bureau for studies on mortality of fingerlings in turbines of hydroelectric dams on the Columbia and Snake rivers. The fluorescent pigments have proved to be reliable, easily recognized marks. These studies, each lasting only a few days, gave no opportunity for determining long-term retention of the tattoos. Therefore, two groups of coho fingerlings were marked with fluorescent-pigment tattoos and held in hatchery ponds to determine the effective life of the marks. Because growth during these tests was small (about 45 mm), the effect of growth on mark visibility was not tested. This note presents the data on long-term retention of tattoo marks.

Materials and methods.— Fluorescent pigments used in this investigation are sold under the trade name of Day-Glo[2] (Switzer Brothers, Inc., 1962). The chemical nature of Day-Glo pigments is described by the manufacturer as "a solid solution of fluorescent dyes in melamine sulfonamide-formaldehyde resin." The resin is a glasslike inert material that completely envelops each particle of fluorescent pigment. The effective life of Day-Glo pigments is

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[1] One of the authors (Donaldson) used fluorescent pigments to mark fingerling salmonids at the Coleman Hatchery, Red Bluff, California, in 1962 for fingerling mortality studies in the turbines of Shasta Dam. The research was sponsored by the U.S. Army Corps of Engineers, Walla Walla District, Walla Walla, Washington.

[2] Trade names referred to in this publication do not imply endorsement of commercial products by the U.S. Bureau of Commercial Fisheries.

J. Fish. Res. Bd. Canada, 25(10): 2233–2236, 1968.
Printed in Canada.

governed by the amount of UV radiation received; the pigments are rated for either 6 or 12 months of outdoor use before noticeable fading. Because water inhibits the penetration of UV rays, tattoo marks of this material on fish are subjected to less exposure and therefore should last longer than the rated life.

The Day-Glo pigments were obtained in insoluble powder form and mixed with water to form a thick paste. Thorough mixing, which is necessary to prevent clogging of the tattoo needles, was difficult by hand stirring, but easy with a blender. The two types of tattooing machines used were described by Chapman (1957) and Volz and Wheeler (1966). The UV light source was a General Electric 15-w "black-light" tube, number F15T8-BLB (3200–4000 Å). When the UV light was on, the fish were examined in an enclosure to shield direct rays of visible light and to increase the brilliance of the fluorescent-pigment tattoos.

Ulceration, a potential cause of fish mortality and mark degeneration, was minimized by adjusting the needles of the marking machines to restrict penetration to skin depth. The first few fish marked were killed and the tattooed portions of the skin carefully separated from the flesh and folded back. Exposure to UV light revealed minute quantities of pigment in the flesh that were invisible under normal light. Needle penetration was considered satisfactory when the tattoo mark was highly visible on the inner surface of the skin, and only minute quantities of pigment (or none) were visible in the flesh.

Two groups of coho fingerlings of the same stock and year-class were marked and held in a pond at the hatchery of the Fish Commission of Oregon at Bonneville Dam, Bonneville, Ore. The first group (group I), marked in December 1963 as underyearlings, consisted of about 500 fish. Group II, marked in April 1964 as yearlings, consisted of about 3000 fish. The Day-Glo pigments injected were aurora pink, signal green, and arc yellow — all rated for 6 months of effective Non-Fade life under outdoor conditions.

In December of 1964, high water conditions in Tanner Creek, which provides water for the hatchery, flushed a considerable portion of the original test population from the holding pond. Periodic checks of mortality did not reveal more than normal hatchery mortality until the fish approached the end of their life expectancy, when mortality increased.

The remaining fish from both groups were examined carefully in July 1965, after group I had been marked 19 months, and group II 15 months. Fish of both groups then averaged 165 mm (fork length) — a growth of about 45 mm from the time of marking for group II, and slightly more than 45 mm for group I.

All fish were first examined under visible light (daylight), and then under UV light. Visibility of the tattoo marks was classed as follows: good — readily visible without close examination; fair — recognizable with close examination; poor — recognizable only with difficulty; and invisible — not recognizable.

Retention of tattoos.— Although many of the tattoos were not visible when viewed in daylight (45.6% from group I and 77.9% from group II), all fish had tattoos that were visible under UV light (Table I). Under UV light, most of the tattoos were classed good (77.2% of group I and 87.0% of group II); the remainder were classed fair or poor.

TABLE I. Percentages of fluorescent-pigment tattoos in various classes of visibility of coho salmon 19 months (group I) and 15 months (group II) after marking as fingerlings.

			Visibility of tattoo marks			
Light source	Color of mark	Total fish	Good	Fair	Poor	Invisible
			19-month group			
Daylight	Green	17	0.0	17.6	23.5	58.8
	Pink	31	9.7	45.2	19.4	25.8
	Yellow	9	11.1	0.0	0.0	88.9
Total/avg		57	7.0	29.9	17.5	45.6
Ultraviolet	Green	17	70.6	23.5	5.9	0.0
	Pink	31	93.5	3.2	3.2	0.0
	Yellow	9	33.3	11.1	55.6	0.0
Total/avg		57	77.2	10.5	12.3	0.0
			15-month group			
Daylight	Green	331	0.0	7.9	4.9	87.3
	Pink	271	1.5	24.7	7.4	66.4
Total/avg		602	0.7	15.4	6.0	77.9
Ultraviolet	Green	331	90.3	7.6	2.1	0.0
	Pink	271	83.0	11.8	5.2	0.0
Total/avg		602	87.0	9.5	3.5	0.0

After the complete check in July 1965, samples of fish from both groups were inspected intermittently. The last sample was taken in May 1966. (An operational breakdown shortly thereafter caused the loss of all fish.) By this time, fish of group I had been marked 29 months, and fish of group II 26 months. All of the 200 fish inspected had visible tattoo marks when viewed under UV light.

The tattoo marks were not completely sloughed by the fingerlings in 19 months and can be expected to remain visible much longer when viewed under ultraviolet light. Retention of fluorescent-pigment tattoos appears to be much greater than that of tattoos of nonfluorescent pigments reported in the literature.

Although the retention of marks reported in these tests was good, growth of the fish may reduce the density and consequently the visibility of the pigment (Kelly, 1967).

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Are Columbia Upriver Salmon Stocks Doomed?

A BCF RESEARCH REPORT

By Wesley J. Ebel & Roger E. Pearson

Many people in Washington and Oregon have said, "Why not forget the upstream stocks of Columbia River salmon? The dams and reservoirs on the Columbia and Snake Rivers will eventually destroy these fish; we should direct all our effort toward increasing the production of salmon from hatcheries on the lower part of the river." Recent information from studies on the Columbia by the Bureau of Commercial Fisheries (BCF) implies that all is not lost. These studies show that downstream survival of wild juvenile fall and spring chinook salmon can be increased by transporting the migrating juveniles around certain dams and reservoirs.

The increase in survival of young fish indicates that upon their return to fresh water in future years, more adult fish will be available to upriver areas to spawn. The crucial point in the method, however, is whether the act of transporting juvenile salmon around points of the river through which they usually migrate will impair their ability to home to their natal spawning areas. Although the final evaluation of this transport system is awaiting the return and upstream migration of marked fish released in a recent transportation experiment, one major step in maintaining upriver runs of salmon has been completed.

In one experiment 200,000 young wild spring chinook salmon were collected and marked at Ice Harbor Dam. About half of these fish were released at Ice Harbor Dam, and the other half were transported downstream by truck and released below John Day and Bonneville Dams (Figs. 2 and 3). Next, the BCF sampled the downstream migration at The Dalles Dam and in the estuary near Astoria, Oregon, for marked fish; the number of recaptured fish that were released at Ice Harbor Dam was then compared with the number of recaptured fish that were transported. Twice as many transported fish reached The Dalles Dam and Astoria. Evidently large numbers of juveniles released at Ice Harbor Dam failed to reach the lower part of the river.

The number of wild chinook salmon available to the commercial and sport fishery could be substantially increased if sufficient numbers of migrating juvenile fish were collected and transported around some of the dams and reservoirs. For example, about 12 million juvenile chinook salmon were estimated to have passed Ice Harbor and Priest Rapids Dams in 1967;

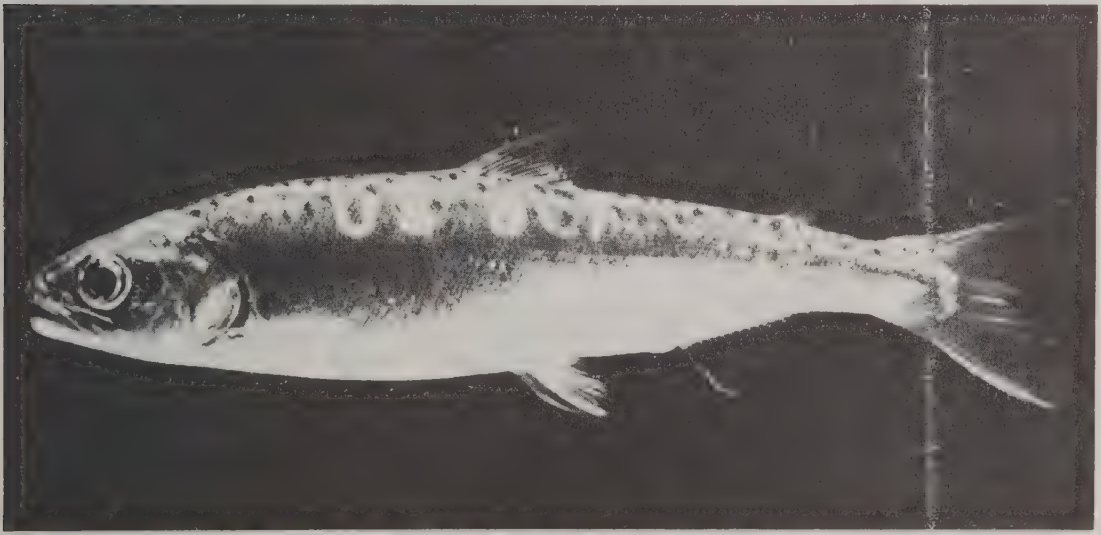

Figure 1.—Juvenile salmon with the type of mark (a thermal brand) that was placed on the young fish. This method of marking salmon was perfected by BCF biologists and is now in wide use throughout the Pacific Northwest.

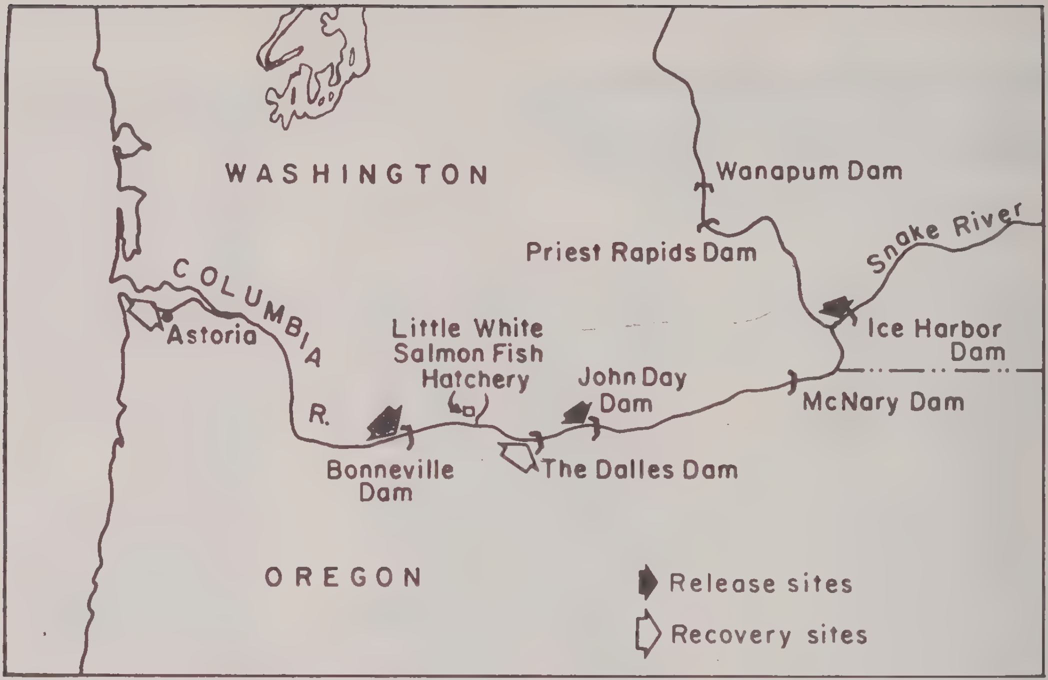
WASHINGTON
OREGON
COLUMBIA R.
Astoria
Little White Salmon Fish Hatchery
Bonneville Dam
The Dalles Dam
John Day Dam
McNary Dam
Ice Harbor Dam
Priest Rapids Dam
Wanapum Dam
Snake River
Release sites
Recovery sites

Figure 2.—Map of the Columbia River showing the location of release sites, dams, and recovery sites.

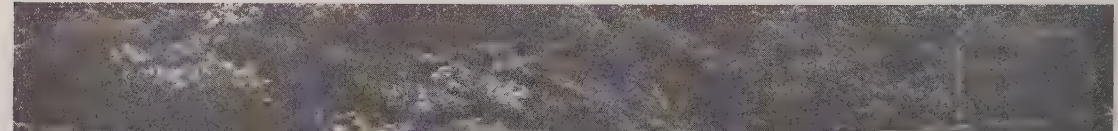

Figure 3.—A 5,000-gallon tank truck used by the BCF to transport juvenile salmon down the Columbia River. The truck carried about 4,000 lbs. of fish (400,000 fish, 2½ inches long).

from our data, we believe that 50 percent of the run failed to reach John Day Dam. Assuming that 25 percent of the 12 million fish could have been transported below John Day, an additional 150,000 salmon would have been available to the commercial and sports fishery if 10 percent of the transported fish had survived their early life in the ocean.

Experiments with hatchery-reared salmon also show that transporting migrating juvenile fish may be beneficial. Results of one study with fall chinook salmon migrating from Little White Salmon National Hatchery indicate that survival in that part of the river between the hatchery and Bonneville Dam could be tripled if the fish were released below Bonneville Dam rather than at the hatchery.

Information on survival to the estuary is being obtained from the BCF research station at Astoria, Oregon. Mr. Carl Sims, Project Leader at Astoria, developed a sampling system in which large numbers of wild and hatchery salmon could be captured near the end of their downstream migration. This system enables biologists to evaluate experiments on downstream survival of different stocks of fish. In the past this evaluation could only be made 2 or 3 years after the downstream migration; estimates of survival had to be based on the number of marked adults returning to the river to spawn.

It may be possible to divert and capture large numbers of downstream migrating salmon at dams on the Columbia River. Bureau scientists have determined that about 70 percent of the downstream migrants are within 15 feet of the ceiling of the turbine intake (fig. 4). Studies at North Bonneville and Pasco, Washington, indicate that a majority of these migrating juveniles could be diverted into turbine intake gatewells from which they could be removed and transported downstream. An increase of 10,000 chinook salmon in the commercial and sport fishery could probably compensate for a transportation system.

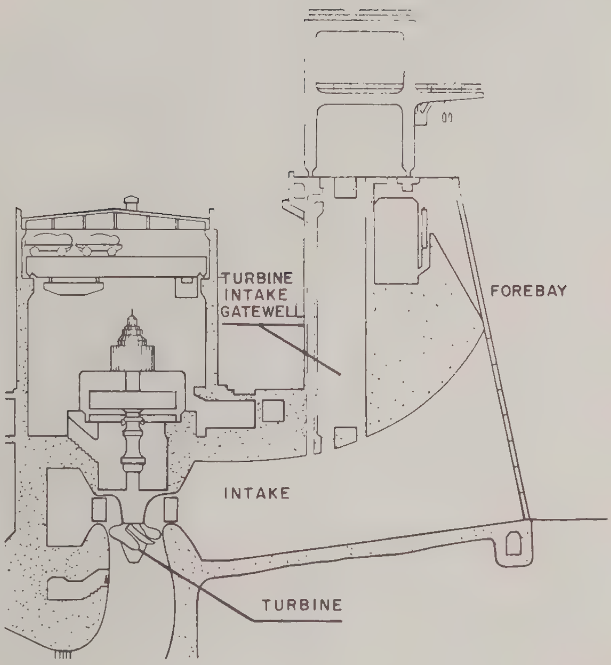

Figure 4.—Location of the turbine intake gatewells in a typical Columbia River dam.

The results of all these studies—the collection of juvenile salmon in gatewells, transportation experiments, and the development of a method to evaluate the transportation experiments in the estuary—provide fishery biologists a new optimism concerning the potential of increasing the numbers of salmon from the upper and lower parts of the Columbia River. Bureau biologists believe that the stocks of salmon in the upper river may not be doomed; the runs can be maintained, and some of them increased, if the knowledge presently being gained on collecting and transporting juvenile salmon is implemented and if transportation does not affect their homing ability.

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ABSTRACT

THE ENZYME HISTOCHEMISTRY OF THE SPORULATION OF *MINCHINIA NELSONI* IN *CRASSOSTREA VIRGINICA*[1]

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Five enzymes were surveyed for reactivity throughout the sporulation process of *Minchinia nelsoni* in *Crassostrea virginica:* NAD diaphorase, non-specific esterase, acid and alkline phosphatase and malic dehydrogenase. Plasmodia and sporonts were generally reactive for all the enzymes studied. There was usually a marked increase in enzyme activity in the sporont stage relative to the plasmodium; this was probably associated with an increase in metabolic activity as the sporulation process started. Early sporocysts manifested a strong activity for mitochondrial enzymes, NAD diaphorase and malic dehydrogenase, but appeared less reactive for the other enzymes. The cytoplasm of the later sporocyst became quite reactive for alkaline phosphatase, concentrations of which could be seen clinging to the cytoplasm surrounding the mature spore walls. Acid phosphatase present a similar picture. Mitochondrial enzymes appeared highly reactive in the cytoplasm of the sporocyst especially in the immediate vicinity of the spore, but sparsely distributed in the sporoplasm of the mature spore; usually 2-6 mitochondria could be observed per spore. Concentrations of non-specific esterase fell sharply as the sporocyst matured, although isolated granules were observed in the cytoplasm of the sporocyst as well as the sporoplasm of the mature spore.

Oyster tissues infected with the sporulating stages of *Minchinia nelsoni* (tubules of the digestive gland) appeared to maintain a near-normal level of enzyme activity; however, heavy concentrations of the parasite all but replaced host tissue, leaving little glandular tissue available for digestion.

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[1] This research was supported by Contract 14-17-0003-111 with the U. S. Bureau of Commercial Fisheries.

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pp. 406–407

TWO HERMAPHRODITIC ALEWIVES FROM LAKE MICHIGAN.—Hermaphroditism has been reported frequently among many of the Clupeidae (Atz, 1964), but only one account of hermaphroditism has been published for the alewife, *Alosa pseudoharengus.* Rothschild (1966) discovered four hermaphroditic alewives among 444 fish he examined from Cayuga Lake, New York.

We recently collected two hermaphroditic alewives from Lake Michigan. Both fish were normal in external appearance but were easily identified as hermaphrodites by gross examination of their gonads. The gonads were preserved in 10% formalin, sectioned in paraffin, and stained with haematoxylin and eosin for histological examination.

The first hermaphrodite (177 mm T.L.) was discovered among several hundred normal adult alewives captured in early July 1965 in the Kalamazoo River about one mile upstream from Lake Michigan. The fish was in spawning condition (Fig. 1) and eggs and sperm could be expressed from it simultaneously. The eggs appeared to be normal but expanded rapidly and burst when placed in water, suggesting the lack of a functional perivitelline membrane. Dissection showed that the left gonad was a normal testis, and the right one was an ovotestis. A sharp constriction between testicular and ovarian portions separated the ovotestis into two discrete lobes. The testicular lobe was anterior and was approximately one-half the length of the ovarian lobe (Fig. 1). Histological examination showed clearly that ovarian and testicular tissue did not intermingle in the ovotestis. The testicular part of the ovotestis and the left testis contained sperm concentrations and were indistinguishable from normal testes.

Only fragmented sections were obtained of the ovarian lobe of the ovotestis because most of the eggs had been expelled and the ovary wall was extremely thin and flaccid. Although the histological organization of the ovarian portion of the ovotestis could not be determined, the rapid disintegration of the eggs in water indicated that the fish was probably incapable of functioning as a female. Little doubt exists, however, that the fish was potentially a functional male, although no attempt was made to use its sperm to fertilize the eggs of a normal female.

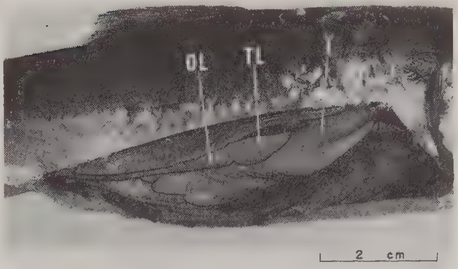

Fig. 1. Hermaphroditic alewife. Left gonad (T) is a normal testis; right gonad is an ovotestis with ovarian (OL) and testicular (TL) lobes.

Only one of the hermaphroditic alewives discovered by Rothschild (1966) had an ovotestis; each of the other three had an ovary and a testis. The ovotestis of the Lake Michigan hermaphroditic alewife captured in 1965 was similar to the one described by Rothschild except that the positions of ovarian and testicular lobes were reversed.

The second hermaphroditic alewife (152 mm T.L.) was obtained from a sample of 160 adult alewives captured in Lake Michigan near the mouth of the Kalamazoo River in mid-April 1966. The fish was mature but was not in spawning condition. Unfortunately, the right gonad was discarded before we realized that the fish was an hermaphrodite. The left gonad was an ovotestis. Histological examination revealed that the most anterior portion of the gonad was entirely ovary and contained young or resting oocytes and ova in fairly advanced stages of development. Testicular tissue appeared near the middle of the gonad and

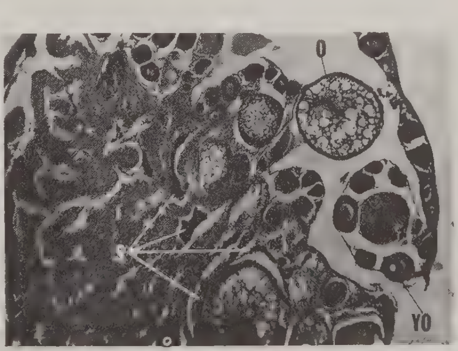

Fig. 2. Posterior portion of ovotestis of hermaphroditic alewife showing young oocytes (YO), developing ova (O), and sperm concentrations (S).

increased posteriorly; the posterior one-third of the gonad was approximately 75% testicular. Ovarian and testicular tissue intermingled slightly (Fig. 2) but the two tissues were much more discrete than they originally appeared under gross examination of the intact gonad. The testicular tissue contained sperm concentrations and was identical to that of a normal male. Heaviest concentrations of sperm, surprisingly, were immediately adjacent to ovarian tissue (Fig. 2). The histological evidence suggests that this fish was potentially a functional hermaphrodite.

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Gb—12. *Effects of Radiation and Salinity on the Respiration of Brine Shrimp Nauplii*. D. W. ENGEL AND J. W. ANGELOVIC, Bureau of Commercial Fisheries, Radiobiological Laboratory, Beaufort, North Carolina 28516.

Respiration rates and Q_{10}'s of nauplii of the brine shrimp, *Artemia salina*, were affected significantly by the level of radiation, the salinity of the water in which the animals were kept, and by the interaction of these two factors. Irradiated nauplii received doses of ^{60}Co gamma radiation ranging from 10,000–80,000 rads, and were maintained in salinities ranging from 5–200 p.p.t. (parts per thousand). Irradiated nauplii at 5 and 50 p.p.t. respired at rates which were about 5–15% below the control level at all doses. Respiration of brine shrimp maintained at 100 and 150 p.p.t., and irradiated with doses up to 40,000 rads, was accelerated above that of the controls, but those animals which received a dose of 80,000 rads respired at about the same rate as the controls. The respiration of irradiated brine shrimp maintained at 200 p.p.t. was increased by a dose of 10,000 rads, and then decreased with increasing doses of radiation. The most pronounced effect on Q_{10} was at the highest salinity where all Q_{10} values were significantly lower than the controls or irradiated nauplii at the other salinities. (This research was supported through a cooperative agreement between the U. S. Fish and Wildlife Service and the U. S. Atomic Energy Commission.)

Comp. Biochem. Physiol., 1968, *Vol.* 26, *pp.* 749 *to* 752. *Pergamon Press. Printed in Great Britain*

THE INFLUENCE OF SALINITY AND TEMPERATURE UPON THE RESPIRATION OF BRINE SHRIMP NAUPLII

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Abstract—1. Respiration rates of day old nauplii of *Artemia salina* were significantly affected by salinities of 5 to 200 ppt and by temperatures which ranged from 10 to 30°C ($P<0{\cdot}01$).

2. The Q_{10}'s for *Artemia* nauplii were significantly affected by temperature ($P<0{\cdot}01$) and the temperature–salinity interaction ($P<0{\cdot}10$).

INTRODUCTION

HISTORICALLY the brine shrimp, *Artemia salina*, has been categorized as one of the most adaptable aquatic invertebrates. Its ability to adapt to a wide range of salinities and temperatures has made it the dominant species in such rigorous environments as Great Salt Lake, Utah. The ability of brine shrimp to survive in salinities of 10–220 ppt and temperatures of 10–35°C has been examined through observation of the respiration rates of nauplii at different salinities and temperatures. Results of these investigations are contradictory; some investigators have demonstrated an increase in respiration rates with increased salinity (Kuenen, 1939), and others have demonstrated a decrease (Eliassen, 1952). Still others have found no effects of salinity on respiration rates (Kratowich, 1964). The purpose of this investigation was to determine whether temperature and salinity affect the respiration rates of brine shrimp nauplii from the Great Salt Lake stock.

METHODS

The brine shrimp nauplii were hatched in 30 ppt sea water, immediately transferred to sea water of 5, 50, 100, 150 and 200 ppt salinity, and allowed to acclimate overnight at 10°C. All salt solutions were made from a commercial sea salt mixture, the composition of which is similar to Great Salt Lake brine.

After acclimation, aliquots of animals and water from the various salinities were transferred to Warburg-type respiration flasks. Each flask contained 3·0 ml of animals and water and 0·5 ml of 20% KOH in the side arm. All determinations of respiration rates were conducted on a differential respirometer and the flasks were shaken at a rate of 80 beats per minute. Determinations of respiration were made for 1 hr at temperatures of 10, 15, 20, 25 and 30°C. The temperature of the water bath was increased 5°C over a 15-min period between each respiration determination. Respiration rates, Q_{O_2} values, were calculated as μl O_2 consumed per mg dry wt of animal per hr. The Q_{10} values were calculated from Q_{O_2} values for each 5°C increase in temperature by using the van't Hoff equation.

RESULTS AND DISCUSSION

Respiration rates of brine shrimp nauplii decreased with increasing salinity at all five temperatures tested (Fig. 1). A good linear relationship existed between temperature and the respiration rates at each salinity, as shown by the correlation coefficients for each of the regression lines. The change in Q_{O_2} per unit change in temperature—the slopes of the regression lines—decreased with increased salinity (0·89 at 5 ppt, 0·76 at 50 ppt, 0·77 at 100 ppt, 0·54 at 150 ppt and 0·43 at 200 ppt). To determine if the differences between the slopes of the regression lines were real, it was assumed that the respiration rates at each temperature were distributed normally and had equal variances. The data were tested by an analysis of covariance which showed that the slopes were significantly different ($P < 0{\cdot}01$). The relationship demonstrated by these data—that increased salinity causes reduced respiration rates in brine shrimp nauplii—supports the findings of Eliassen (1952) who demonstrated a similar relationship for brine shrimp nauplii at salinities of 10 to 50 ppt. Contrary to our results, however, he found a decrease in respiration with increased temperature from 14 to 22°C. Kratowich (1964), however, found no significant effect of salinity on the respiration of brine shrimp nauplii at salinities up to 90 ppt.

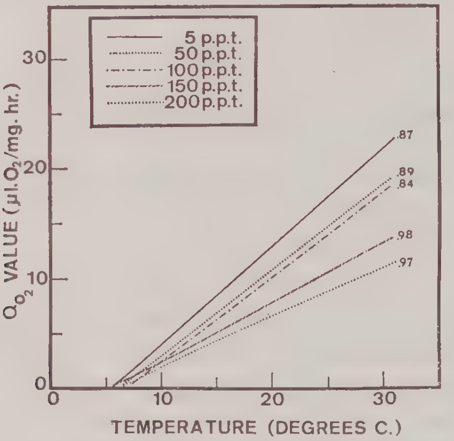

Fig. 1. The effect of temperature upon the respiration rates of brine shrimp nauplii at five salinities. The numbers at the ends of the regression lines are the correlation coefficients for the lines.

The metabolic rates of the nauplii at the five salinities tested in the present experiments approached zero between 5 and 8°C. If it is assumed that the relation between temperature and Q_{O_2} described by the regression equation holds true below 10°C, then the lines intercept the abcissa between 5 and 8°C. It has been shown that when the water temperature in Great Salt Lake falls below 6°C, adult brine shrimp are no longer found and nauplii do not appear in the spring until the temperature returns to 9°C (Relyea, 1937). Thus, the results of our experiments are compatible with the temperatures at which adult brine shrimp disappear and nauplii reappear in Great Salt Lake.

The Q_{10} values for the brine shrimp nauplii were not directly related to the salinity of the medium (Fig. 2). When the Q_{10} values for all temperature–salinity combinations tested were analyzed by an analysis of variance, temperature was found to be a highly significant factor ($P < 0{\cdot}01$), salinity was not significant and the temperature–salinity interaction was significant at the $P < 0{\cdot}10$ level of confidence. The influence of temperature was expected, since temperature affects the rates of biological and chemical reactions. The response of the brine shrimp nauplii to temperature change appears to be almost independent of salinity because the patterns of Q_{10} values are similar for each salinity. The only exception is at the salinity of 150 ppt, at which Q_{10} decreased with increasing temperature. At present we have no explanation for this difference in response to temperature increase.

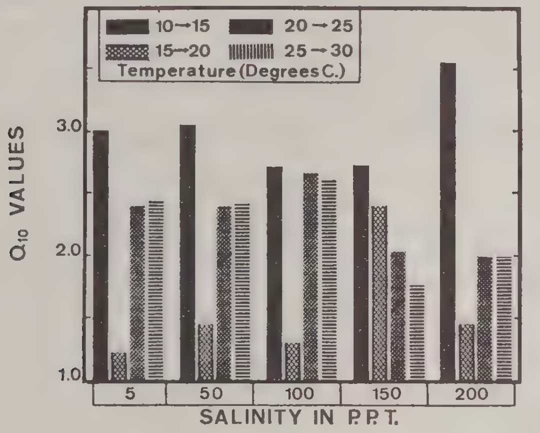

Fig. 2. Q_{10} values for brine shrimp nauplii at five salinities.

The apparent differences in the available data on the effects of temperature and salinity upon the respiration rates of brine shrimp nauplii may result, in part, from genetic differences in the animals. There are many populations of *Artemia* throughout the world, and each of these populations has a slightly different habitat. Thus their physiological responses to changes in the environment, such as changes in temperature and salinity, may be different. This makes it very difficult to compare results of various investigations which use different sources of cysts. A careful examination of the physiological characteristics of each population of *Artemia* is warranted to determine if there is indeed more than one physiological race of *Artemia*. These experiments have demonstrated that temperature and salinity significantly affect the respiration rates of *Artemia* nauplii from Great Salt Lake stock, and that the Q_{10}'s are affected significantly only by temperature.

Acknowledgements—This research was supported through a cooperative agreement between the U.S. Fish and Wildlife Service and the U.S. Atomic Energy Commission (Contract No. AT(49-7)-5). Mr. Kenneth Fischler gave us advice and assistance in the statistical analysis of the data.

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Recurrent Group Analysis of Species Assemblages of Demersal Fish in the Gulf of Guinea[1]

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ABSTRACT

Recurrent species groups were formed by computer analysis from the data on occurrence of demersal fish at 480 trawl stations in the tropical eastern Atlantic; these recurrent groups were then marshalled into a small number of major species assemblages, or communities in the wide sense, on the basis of intergroup relationships. These assemblages proved to be remarkably similar in composition and ecology to the communities of demersal fish recognized earlier by a number of authors from their subjective analysis of trawling survey data in this region. The computer analysis provided finer detail on both the structure and distribution of the assemblages and their constituent groups. This confirmation of the reality of the subjectively recognized communities suggests (1) that the recognition of such assemblages by subjective methods has a place in the assessment of multispecies fish resources but (2) that where the method is practicable, the machine processing of recurrent species groups in the analysis of trawl survey data can be a valuable tool in resource evaluation.

INTRODUCTION

During the last two decades many demersal trawl surveys have been performed by fishery agencies in West Africa to assess the fishery resources of the tropical continental shelf. It became evident during this period of exploration that not only was there a homogeneous fauna of demersal fish the whole length of the tropical Gulf of Guinea but also that there was a considerable degree of agreement among the various authors who had written about it as to how this fauna was organized into recurrent species groups or communities. This agreement is found in the descriptions of the demersal fauna in all 10 of the surveys that were reported in such a manner that their results could be used to identify recurrent species groupings of demersal fish (Table I), although (as can been seen from the tabulation) there was little uniformity in the descriptive terms employed. The species assemblages may be briefly described as follows:

i — Two rather similar assemblages (A and B in Table I), each dominated by species of Sciaenidae, Polynemidae, Ariidae, Cynoglossidae, Pomadasyidae,

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TABLE I. The species assemblages of demersal fish recognised subjectively in the Gulf of Guinea, with the terminology used by each author. (A plus (+) sign indicates that an author recognized an assemblage without applying a descriptive term to it.)

Area and author	Assemblage of demersal fish				
	A	B	C	D	E
Gambia (Longhurst, 1963)	Sciaenid fauna		Sparid fauna		Deep fauna
Guinea (Postel, 1955)	+		+		
Sierra Leone (Longhurst, 1963)	Sciaenid fauna		Sparid fauna		Deep fauna
Ghana (Salzen, 1957)[a]	+		+		+
Ivory Coast (Lassarat, 1957)	+				
Togo and Dahomey (Crosnier and Berrit, 1966)	Peuplement des fonds vasa-sableux baignées par des eaux chaudes	Peuplement des fonds durs baignées par eaux chaudes and Peuplement fonds sableux eaux chaudes		Peuplement des fonds vaseux baignées eaux froides	
Nigeria (Longhurst, 1963)	Offshore sciaenid sub-community	Estuarine sciaenid sub-community	Supra-thermocline sparid community	Sub-thermocline sparid community	Deep community
Cameroon (Crosnier, 1964)	Peuplement des fonds vaso-sableux baignées eaux chaudes		Peuplement des fonds sableux eaux chaudes	Peuplements des fonds vaseux eaux froides	
Congo (Poll, 1951)	Faune côtière			Faune de bordure continentale	Faune de la pente continentale
Congo (Durand, 1966)	Peuplement littoral			Peuplement de bordure continentale	Peuplement du talus continentale

[a] Salzen (1957) also recognized an assemblage (F) at about 400 m and deeper, on the upper continental slope.

Drepanidae, and Clupeidae. These assemblages, one of which occurs on the continental shelf (A) and the other in estuaries (B), differ mainly in the substitution of some closely related species, and in differences in the relative abundance and frequency of some species and genera, in the two types of habitat.

ii — Two assemblages dominated by Sparidae and Denticidae and including a number of species of other families typical of sandy deposits, such as Triglidae, Mullidae, Synodidae, Scorpaenidae, Platycephalidae, and others. The two assemblages were sometimes confused and appear as C and D in Table I. They have different depth distributions, the one (C) above and the other (D) below the thermocline.

iii — An assemblage (E) occurring below the break of slope of the continental shelf at about 60–80 m and extending to 200–300 m depth. Many of the taxa are also found in similar assemblages at similar depths off western Europe. The main genera in this assemblage are *Chlorophthalmus*, *Peristedion*, *Bembrops*, and *Antigonia*.

iv — Deeper yet, near and below 400 m on the upper continental slope, the fauna changes to an assemblage (F) dominated by *Chaunax*, *Halosaurus*, *Epigonus*, *Galeus*, *Citta*, and *Trigla*.

v — Besides the species which most investigators agreed fell into one of the above assemblages, a few, such as *Cynoglossus canariensis* and *Brachydeuterus auritus*, were hard to place in any one assemblage because of their great bathymetric range and apparently wide ecological tolerance; they have been referred to as eurybathic species.

All the above assemblages were recognized on a subjective basis. When the data from the recently completed Guinean Trawling Survey became available, it seemed worthwhile to apply an objective grouping technique (Fager, 1957, 1963) to see whether or not the same assemblage would be obtained by its use and whether finer details of the structure of the communities would be revealed, and to explore more closely than had been previously possible the interrelationships of the assemblages with each other and with their environment. This paper reports the results of this and compares the objective with the subjective groupings: we believe that the results are of general interest for resource assessment studies in demersal fisheries, at any latitude, which are based on multispecies stocks.

MATERIALS

The data available for analysis were the species lists from the many stations worked with otter trawls during the Guinean Trawling Survey (GTS), organized in 1963–64 as Project 19 of the Commission for Technical Cooperation in Africa (CCTA) with its headquarters in Lagos, Nigeria. GTS was performed by two chartered trawlers very closely matched as to fishing power, that worked simultaneously over a pattern of trawl stations disposed along 63 transects spaced at 40-mile intervals the length of the tropical West African coast from Cape Roxo, south of Senegal, to the mouth of the Congo River (Fig. 1). Estuarine regions were not trawled.

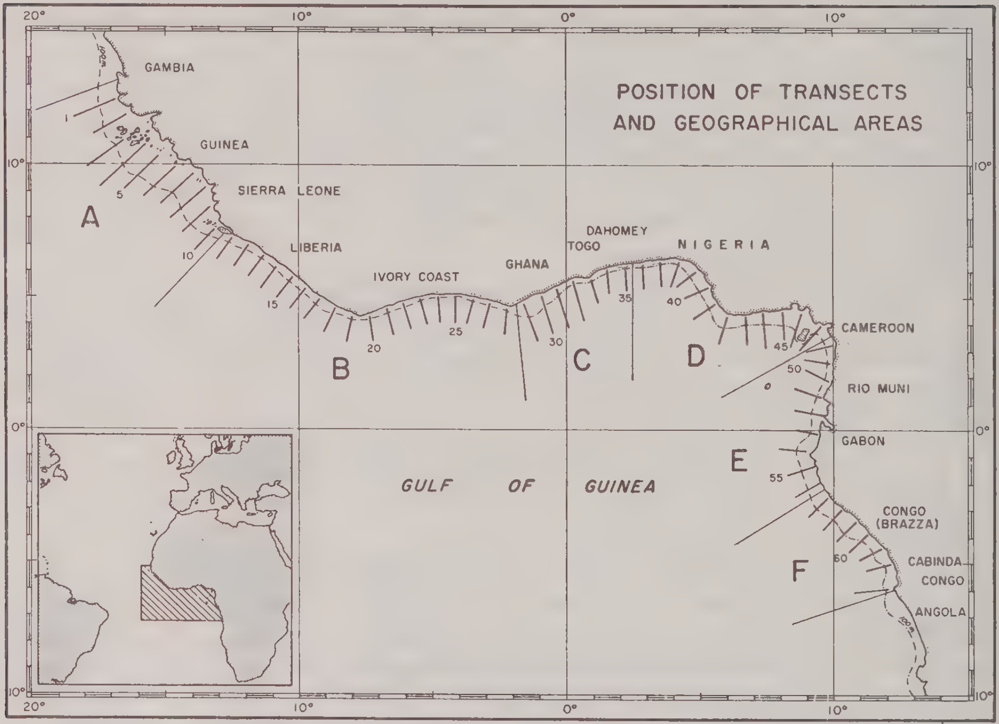
POSITION OF TRANSECTS
AND GEOGRAPHICAL AREAS
GAMBIA
GUINEA
SIERRA LEONE
LIBERIA
IVORY COAST
GHANA
DAHOMEY
TOGO
NIGERIA
CAMEROON
RIO MUNI
GABON
CONGO (BRAZZA)
CABINDA
CONGO
ANGOLA
GULF OF GUINEA
A
B
C
D
E
F
1
5
10
15
20
25
30
35
40
45
50
55
60
20°
10°
0°
10°

FIG. 1. The eastern tropical Atlantic Ocean, showing the location of the 63 transects of the Guinean Trawling Survey and the six subdivisions of this region used here for zoogeographical analysis.

On each transect eight stations were worked at the following series of standard depths: 15–20, 30, 40, 50, 70–75, 150, 250, and 400–600 m. Bathymetric control was very close during each haul and was checked by a bathykymograph mounted on the headrope of the trawl. Each station consisted of a simple suite of hydrographic and biological observations, followed by a 1-hr haul with standard otter trawls having headropes of 25 m and bridles of 37 m. Data derived from a total of 480 such stations were available for this analysis. Because of memory limitations of the computer, only the 175 most frequently occurring taxa in the lists were considered — these taxa were predominantly fish species, though some larger taxonomic units of fish and a single economically important species of penaeid prawn were also included.

GTS consisted of two surveys; Guinean I (GI) during September–December 1963, and Guinean II (GII) during February–May 1964. The first survey was during the transition from the wet to the dry season, soon after the peak effects of runoff from the rains of the preceding 3–4 months, and during a period of steadily rising insolation and mixed-layer temperatures. The second survey was at the height of the dry season, when temperatures would be at a maximum for the year and the influence of freshwater runoff minimal. The area of the survey was almost entirely within the tropical region dominated by the Guinea Current and only marginally within the transitional zones between this current and the eastern boundary currents to the north and south. Within this tropical region, as the description of Berrit (1962) in particular shows, the hydrographic regime is remarkably constant, with the single exception of the localized area of seasonal coastal upwelling off Ghana and the Ivory Coast.

Records of the type of bottom deposit were based on the debris collected in the codend or adhering to the otter boards of the trawl at the end of the haul.

Hard-substrate environments were encountered mostly on inshore rocky reefs (off such localities as the Sierra Leone Peninsula), and on the offshore fossil coral banks that have been found along almost the entire coast near the break of slope on the continental shelf, generally at depths of 60–80 m (Allen and Wells, 1962). The rest of the West African continental shelf is covered by sandy or muddy deposits; the occurrence of mud depends in part on the presence of rivers, although the deposits outside the break in slope of the continental shelf are almost invariably muds. Because of the effluents of the Niger, Cross, Cameroon, and Congo rivers, bottom deposits at depths less than 80 m in the area east of Cotonou were predominantly muddy (90% of stations); to the west of Cotonou sand and rocks were much more frequent (43% of stations) at those depths.

METHODS

The computer program for grouping of taxa (REGROUP) was described by Fager (1957, 1963). It uses as an index of affinity the geometric mean of the proportion of joint occurrences, based on records of presence and absence, and is corrected for sample size. In the present study, the value of 0.5 was used as a breakpoint, only indices above this value being considering evidence of affinity. Thus, species whose frequencies of occurrence differed by more than a factor of four would not show affinity. The formation of recurrent groups was based primarily on two rules: firstly, that every taxon within a group must show affinity with all other members of the group, thus ensuring that every taxon in a group frequently co-occurs with every other member; secondly, that the largest possible groups must be formed. Species that showed affinity with some, but not all, of the members of a group were listed as associates of the group.

After the recurrent groups were formed, the connections between them were determined in terms of the number of species in each group that showed affinity with species in other groups (CONNEX). These are reported as fractions of possible connections, e.g., for two groups of three or four species each, there are 12 possible connections; an intergroup connection would be considered present and meaningful if at least three (0.25 of possible) intergroup pairs of species showed affinity. The distributions of occurrences of groups among the stations were also listed (STATION).

The recurrent groups were formed separately for GI and GII. In both surveys, over half of the taxa (91 and 97, respectively) did not occur consistently enough with others to show affinity at the level chosen. The taxa that did show affinity at this level (84 and 78) were either assigned to groups or noted as associates of these groups.

A comparison of the composition of the recurrent groups derived from the REGROUP program for GI and GII is made in Table II. Although only two groups (15 and 20) were identical in both surveys, most could be recognized in both on the basis of having at least some taxa in common, especially when associates were considered.

Most of the differences between the two surveys involved only changes in apportionment of taxa among groups shown to be related by CONNEX and STATION. Groups 1–3 provide a good example: in GI most of the taxa were put in group 1, whereas in GII they were distributed more evenly among all three groups. There were just two exceptions to this general rule: three groups (GI 13 and 17, GII 21) could not be matched between the surveys because the taxa included had significant affinity indices on only one survey; two taxa, *Sphyraena* spp. and *Lagocephalus laevigatus*, were put in group 19 in GII and were, respectively, a member and an associate of group 7 in GI. Because, as will be shown below, these two groups are members of two distinct multigroup assemblages, this difference appears to be evidence of a real seasonal shift in distribution. The other shifts between groups may also represent small seasonal changes in distribution or may be only the result of sampling variability. We cannot discriminate between these two possibilities on the basis of the present data.

Inspection of the lists of recurrent groups shows at once that they are considerably more numerous than are the subjective assemblages derived from previous work (Table I). To form larger assemblages that might correspond with the subjective communities, two ways of combining groups were tested, neither seeming at first sight to be of greater validity than the other: firstly, groups were combined on the basis of the species connections between them (CONNEX) when these reached a value of at least 0.25; secondly, combination was on the basis of frequency of joint occurrence of the groups (STATION) on individual transects, irrespective of the depth of haul. In this second method, groups were combined in an assemblage when they occurred jointly on transects more often than expected by chance (expectation based on total frequencies of occurrence; tested by chi square on 2 × 2 tables). The results of these two operations are summarized in Fig. 2 and 3, in which the assemblages have been arranged with the shallow-water groups near the top of the figure and the deepwater groups near the bottom.

In both surveys, only a few groups (GI 10, 13, 14, and GII 10, 12) were not marshalled into larger assemblages by connections based on affinities between component taxa. This method of forming assemblages tended to combine groups with similar depth ranges (cf. Fig. 2 and 3) and the groups show close agreement with the subjectively recognized communities listed in

TABLE II. Composition of the recurrent species groups (REGROUP), indicating differences between the two cruises. The numbers after the broken lines in the lists indicate the placing of a taxon in the other survey; e.g., the number 6 in group 1 of GI indicates that *Cynoglossus canariensis* was put in group 6 of GI.

Group no.	Guinean I	Guinean II
1	*Brachydeuterus auritus*	*Brachydeuterus auritus*
	Galeoides decadactylus	*Galeoides decadactylus*
	Vomer setapinnis	*Vomer setapinnis*
	Pseudotolithus senegalensis	*Pseudotolithus senegalensis*
	Ilisha africana	*Ilisha africana*
	Arius spp.	– – – – 3
	Pteroscion peli	– – – – 3
	Drepane africana	– – – – 2
	Pomadasys jubelini	– – – – 2
	– – – – 6	*Cynoglossus canariensis*
2	– – – – 1	*Deprane africana*
	– – – – 1	*Pomadasys jubelini*
3	*Pseudotolithus typus*	*Pseudotolithus typus*
	Dasyatis margarita	– – – –
	– – – – 1	*Arius* spp.
	– – – – 1	*Pteroscion peli*
	– – – – 4	*Pentanemus quinquarius*
4	*Pentanemus quinquarius*	– – – – 3
	Cynoglossus browni	– – – –
5	*Scoliodon terranovae*	*Scoliodon terranovae*
	Ephippion guttifer	– – – – 1 assoc.
	– – – – 6	*Penaeus duorarum*
	– – – – 7	*Paragaleus gruveli*
6	*Penaeus duorarum*	– – – – 5
	Cynoglossus canariensis	– – – – 1
	Trichiurus lepturus	– – – – 1 assoc.
7	*Paragaleus gruveli*	– – – – 5
	Sphyraena spp.	– – – – 19
8	*Dentex angolensis*	*Dentex angolensis*
	Dentex congoensis	*Dentex congoensis*
	Paracubiceps ledanoisei	– – – – 8 assoc.
	Lepidotrigla laevispinis	– – – –
	Squatina oculata	– – – – 9
	– – – – 8 assoc.	*Lepidotrigla cadmani*
	– – – – 8 assoc.	*Eucitharus linguatula*
9	*Pentheroscion mbizi*	*Pentheroscion mbizi*
	Brotula barbata	– – – – 9 assoc.
	– – – – 8	*Squatina oculata*
10	*Peristedion cataphractum*	*Peristedion cataphractum*
	Zenopsis conchifer	*Zenopsis conchifer*
	Antigonia capros	– – – – 10 assoc.
	Synagrops microlepis	– – – –
	– – – – 10 assoc.	*Bembrops heterurus*

(*Continued*)

TABLE II. Composition of the recurrent species groups (REGROUP), indicating differences between the two cruises. The numbers after the broken lines in the lists indicate the placing of a taxon in the other survey; e.g., the number 6 in group 1 of GI indicates that *Cynoglossus canariensis* was put in group 6 of GI. — (*Concluded*)

Group no.	Guinean I	Guinean II
11	*Chaunax pictus*	*Chaunax pictus*
	Epigonus telescopus	*Epigonus telescopus*
	Moridae	Moridae
	Macrouridae	Macrouridae
	Benthodesmis	– – – – 11 assoc.
	Galeus polli	– – – – 11 assoc.
	Setarches guentheri	– – – –
	Merluccius spp.	– – – –
	– – – – 11 assoc.	*Dibranchus atlanticus*
	– – – – 12	*Aristeus varidens*
12	*Cyttus roseus*	*Cuttys roseus*
	Aristeus varidens	– – – – 11
	Halosaurus oweni	– – – – 11 assoc.
	Etmopterus pusillus	– – – –
	– – – –	*Paracubiceps multisquamis*
13	*Trachinocephalus myops*	– – – – No similar
	Bothus podas africanus	– – – – group
	Xyrichthys novacula	– – – –
14	*Lutjanus fulgens*	– – – – No similar
	Bodianus iagonensis	– – – – group
15	*Lathrinus atlanticus*	*Lrtheinus atlanticus*
	Balistes forcipatus	*Balistes forcipatus*
16	*Acanthurus monroviae*	*Acanthurus monroviae*
	Lutjanus agennes	– – – – 16 assoc.
	– – – –	*Chaetodon luciae*
17	*Pagrus ehrenbergi*	– – – – 19
	Chilomycterurus spp.	– – – –
18	– – – – 19 assoc.	*Dactylopterus volitans*
	– – – –	*Balistes capriscus*
19	*Priacanthus arenatus*	*Priancathus arenatus*
	Fistularia villosa	*Fistularia villosa*
	Pseudupeneus prayensis	*Pseudupeneus prayensis*
	Pagellus coupei	*Pagellus coupei*
	Raja miraletus	*Raja miraletus*
	Ephinephelus aeneus	– – – – 19 assoc.
	– – – – 17	*Pagrus ehrenbergi*
	– – – – 7	*Sphyraena* spp.
	– – – – 7 assoc.	*Lagocephalus laevigatus*
20	*Boops boops*	*Boops boops*
	Scomber japonicus	*Scomber japonicus*
	Trachurus spp.	*Trachurus* spp.
21	– – – – No similar	*Hypoclydonia bella*
	– – – – group	*Chascanopsetta lugubris*

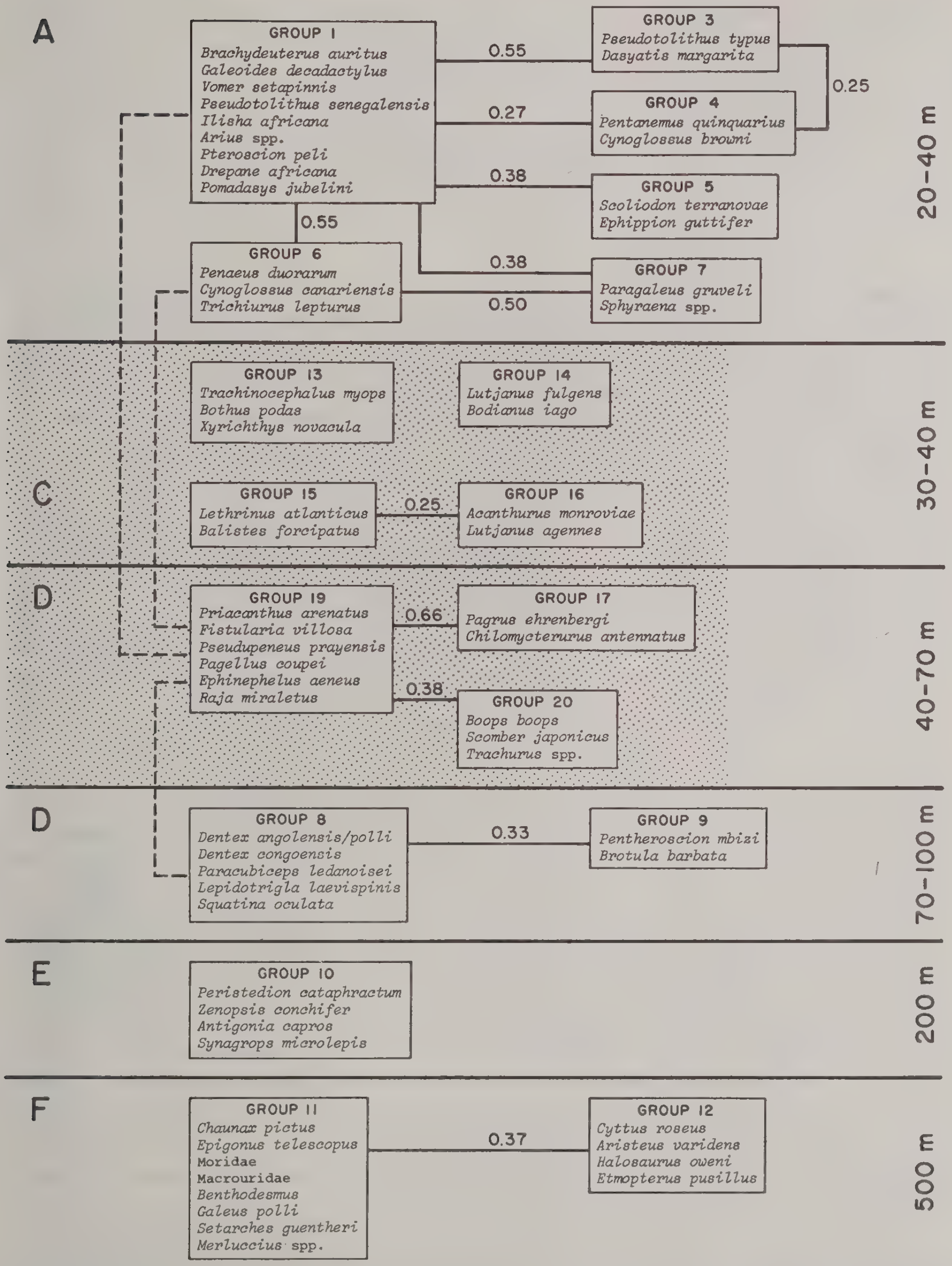
A
GROUP 1
Brachydeuterus auritus
Galeoides decadactylus
Vomer setapinnis
Pseudotolithus senegalensis
Ilisha africana
Arius spp.
Pteroscion peli
Drepane africana
Pomadasys jubelini
0.55
GROUP 3
Pseudotolithus typus
Dasyatis margarita
0.25
0.27
GROUP 4
Pentanemus quinquarius
Cynoglossus browni
0.38
GROUP 5
Scoliodon terranovae
Ephippion guttifer
0.55
GROUP 6
Penaeus duorarum
Cynoglossus canariensis
Trichiurus lepturus
0.38
0.50
GROUP 7
Paragaleus gruveli
Sphyraena spp.
20–40 m
GROUP 13
Trachinocephalus myops
Bothus podas
Xyrichthys novacula
GROUP 14
Lutjanus fulgens
Bodianus iago
C
GROUP 15
Lethrinus atlanticus
Balistes forcipatus
0.25
GROUP 16
Acanthurus monroviae
Lutjanus agennes
30–40 m
D
GROUP 19
Priacanthus arenatus
Fistularia villosa
Pseudupeneus prayensis
Pagellus coupei
Ephinephelus aeneus
Raja miraletus
0.66
GROUP 17
Pagrus ehrenbergi
Chilomycterurus antennatus
0.38
GROUP 20
Boops boops
Scomber japonicus
Trachurus spp.
40–70 m
D
GROUP 8
Dentex angolensis/polli
Dentex congoensis
Paracubiceps ledanoisei
Lepidotrigla laevispinis
Squatina oculata
0.33
GROUP 9
Pentheroscion mbizi
Brotula barbata
70–100 m
E
GROUP 10
Peristedion cataphractum
Zenopsis conchifer
Antigonia capros
Synagrops microlepis
200 m
F
GROUP 11
Chaunax pictus
Epigonus telescopus
Moridae
Macrouridae
Benthodesmus
Galeus polli
Setarches guentheri
Merluccius spp.
0.37
GROUP 12
Cyttus roseus
Aristeus varidens
Halosaurus oweni
Etmopterus pusillus
500 m

FIG. 2. The composition of species groups from GI and their marshalling into major assemblages or communities. Lines linking the groups indicate intergroup affinities; where the value from CONNEX equals or exceeds 0.25 it is indicated numerically on the lines that link the groups; broken lines indicates values less than 0.25. The stippled area of the figure indicates the second assemblage given by the analysis based on common occurrence on transects (STATION).

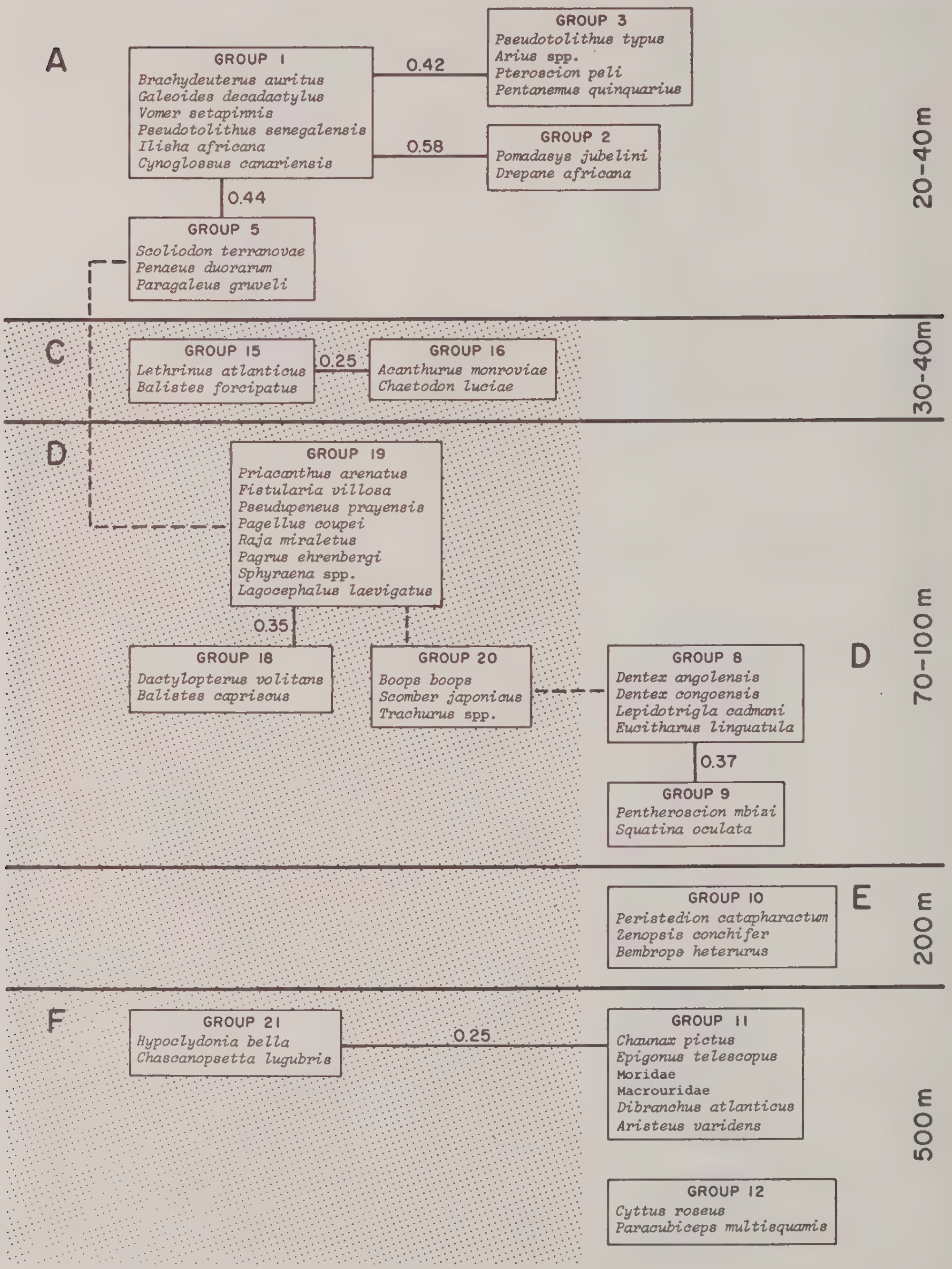
A
GROUP 1
Brachydeuterus auritus
Galeoides decadactylus
Vomer setapinnis
Pseudotolithus senegalensis
Ilisha africana
Cynoglossus canariensis
0.42
GROUP 3
Pseudotolithus typus
Arius spp.
Pteroscion peli
Pentanemus quinquarius
0.58
GROUP 2
Pomadasys jubelini
Drepane africana
0.44
GROUP 5
Scoliodon terranovae
Penaeus duorarum
Paragaleus gruveli
20-40m
C
GROUP 15
Lethrinus atlanticus
Balistes forcipatus
0.25
GROUP 16
Acanthurus monroviae
Chaetodon luciae
30-40m
D
GROUP 19
Priacanthus arenatus
Fistularia villosa
Pseudupeneus prayensis
Pagellus coupei
Raja miraletus
Pagrus ehrenbergi
Sphyraena spp.
Lagocephalus laevigatus
0.35
GROUP 18
Dactylopterus volitans
Balistes capriscus
GROUP 20
Boops boops
Scomber japonicus
Trachurus spp.
GROUP 8
Dentex angolensis
Dentex congoensis
Lepidotrigla cadmani
Eucitharus linguatula
D
0.37
GROUP 9
Pentheroscion mbizi
Squatina oculata
70-100 m
GROUP 10
Peristedion cataphractum
Zenopsis conchifer
Bembrops heterurus
E
200 m
F
GROUP 21
Hypoclydonia bella
Chascanopsetta lugubris
0.25
GROUP 11
Chaunax pictus
Epigonus telescopus
Moridae
Macrouridae
Dibranchus atlanticus
Aristeus varidens
500 m
GROUP 12
Cyttus roseus
Paracubiceps multisquamis

FIG. 3. The composition of species groups from GII and their marshalling into major assemblages or communities. Lines linking the groups indicate intergroup affinities; where the value from CONNEX equals or exceeds 0.25 it is indicated numerically on the lines that link the groups; broken lines indicate values less than 0.25. The stippled area of the figure indicates the second assemblage given by the analysis based on common occurrence on transects (STATION).

Table I. (The letters on the figures indicate the relationships; assemblage B does not occur on Fig. 2 and 3 because the surveys did not extend into estuarine environments.)

The analysis based on joint occurrences of groups on transects resulted in the formation of only two assemblages (in Fig. 2 and 3 and Table III). Groups placed in different assemblages occurred together on transects less often then expected by chance; consequently this second method of analysis tended to put together groups that occurred over similar substrates (cf. Table III, last column).

It is evident from Fig. 2 and 3 that although the two methods of combining groups gave different results, the major difference is one of scale, the method using intergroup affinities produced more, and smaller, assemblages. In only one case (groups 11 and 21 in GII) did one method suggest a connection where the other suggested a separation. Both methods separated the subjectively formed assemblage D into two components. Both methods gave remarkably similar results with the independent sets of data from the two cruises, GI and GII; most of the intercruise differences between the assemblages being similar in nature to the differences between groups on the two cruises. Because the two methods of forming assemblages emphasize different aspects of the environment, they give complementary results. Because the method using intergroup species affinities gives more detail, it may be the method of choice in future employments of this method of analyzing species assemblages.

COMPARISON OF OBJECTIVE AND SUBJECTIVE GROUPINGS

Most of the assemblages based on intergroup species affinities showed no connections, although assemblages A and D were exceptional in that a few species of one group in A (6 in GI, 5 in GII) had affinities at less than the 0.25 level with some species of group 19 in D. Several of these species in groups 5 and 6 (*Cynoglossus canariensis*, *Trichiurus lepturus*, *Scoliodon terranovae*, *Penaeus duorarum*, and *Paragaleus gruveli*) were previously considered as eurybathic and unassigned to a community. The results of the present analysis confirm that they have a wide depth range, but occur most frequently at depths between those favored by most of the groups in assemblage A and most of those in assemblage D.

An examination of the species groups forming assemblage A reveals only one group with any evident ecological significance: that which contains *Pseudotolithus typus* in each set of data. This sciaenid occurs more frequently in estuaries than on the open shelf, and it is significant that it occurs together with *Dasyatis margarita* in GI and with *Arius* spp., *Pteroscion peli*, and *Pentanemus quinquarius* in GII, for all of these are also normally common in estuarine samples. The two groups (GI 3 and GII 3), therefore, may represent the fauna which was taken on the shelf in both seasons when estuarine conditions were approached, and previously termed the estuarine sciaenid subcommunity.

TABLE III. The composition and ecological distribution of species groups. *No. stations* = number at which the whole group occurred together; *temperature range and depth distribution* = medians and ranges, as relevant; *geographic distribution*: A = transects 1–10 (Cape Roxo to Freetown), B = 11–28 (Freetown to Cape Three Points), C = 29–35 (Cape Three Points to Cotonou), D = 36–47 (Cotonou to Douala), E = 48–56 (Douala to Cape Lopez), and F = 57–63 (Cape Lopez to Congo River); *bottom deposit*: M = mud, SM = sandy-mud and muddy-sand, S = sand, SR = sand and gravel or rocks, R = rocks or coral. The broken line separates the two major assemblages based on joint occurrence on transects.

Group	Survey	No. taxa	No. stations	Temp range (*C*)	Depth (*m*)	Geographic distribution	Bottom deposit
1	I	9	30	19–27	20 (15–50)	D,F	
	II	6	45	20–45	30 (15–50)	D,F	M,SM
2	II	2	31	21–30	30 (15–40)		
3	I	2	30	19–28	20 (15–40)	D,F	
	II	4	16	20–29	20 (15–50)	D,F	
4	I	2	17	19–28	20 (15–50)	D,F	
5	I	2	71	18–29	30 (15–70)		SM
6	I	3	63	16–27	40 (15–70)	D	
7	I	2	72	17–27	40 (15–100)	D	
8	I	5	35	14–20	70 (70–200)		
	II	4	50	14–22	100 (40–200)	D,E	
9	I	2	54	14–22	100 (40–200)	D	M
	II	2	55	12–22	100 (50–200)	D	
10	I	4	15	13–16	200 (200–200)		
	II	3	17	12–17	200 (200–200)	E,F	
11	I	8	9	9–10	500 (400–600)		M
	II	6	8	8–10	500 (400–600)	E,F	M
12	I	4	7	9–10	500 (400–600)	D	M
	II	2	14	7–16	500 (200–600)	D,E	M
13	I	3	14	20–27	30 (15–50)	A	S
14	I	2	13	9– 4	40 (15–70)		SR,R
15	I	2	25	17–25	30 (15–50)		S,SR
	II	2	24	18–28	30 (15–40)	A,C	S,SR
16	I	2	13	17–24	40 (15–50)		SR,R
	II	2	13	18–25	40 (15–50)	C	SR
17	I	2	67	19–24	40 (15–70)		SM
18	II	2	44	18–28	40 (15–70)		S,SR
19	I	6	44	17–23	50 (15–70)		
	II	8	31	17–24	50 (15–70)		
20	I	3	45	15–23	70 (40–200)	A,C	SR
	II	3	36	16–21	70 (30–100)		
21	II	2	21	8–16	500 (200–600)		

It is also perhaps significant that the small sand shark *Scoliodon terra-novae* occurs only in small species groups and shows no affinities (though it is a commonly occurring species) with any of those recurrent groups in either cruise which include the bulk of taxa typical of the offshore sciaenid subcommunity. This accords well with the frequently made observation that this species and the normal teleosts of the community tend to be mutually excluding in the trawl catches, perhaps suggesting that when an aggregation of sand sharks moves into an area, the teleosts move out.

Groups 15 and 16 of GI and GII, together with their associated species, clearly from a community that is stable between the two cruises, and corresponds most closely with community C (Table I), the supra-thermocline sparid community of Longhurst (1963). There are, however, certain important differences. The absence of *Pagrus ehrenbergi* and *Albula vulpes* and the restriction of the group to reef-inhabiting species suggest that the shallow-water sparid community proposed by Longhurst was an artificial group; assemblage C as defined by REGROUP evidently represents the fauna occurring on the Holocene coral banks of the continental shelf, where there is known to be a fauna of lutjanids, lethrinids, and other reef fish that were included previously as part of the sparid community. The present analysis indicates that they have no affinity with any other group, and must form an assemblage of their own, to be designated the lutjanid community. The apparent occurrence of these species on a variety of deposit types is not to be taken too seriously, since they were probably caught when a trawl momentarily crossed over, or passed very close to a reef out-cropping from other deposits.

The groups comprising assemblage D require some investigation. In each cruise two groups (17 and 19 in GI, 18 and 19 in GII) occurred at depths and temperatures corresponding to the bottom of the thermocline, yet extended upwards into the mixed layer and temperatures above 25 C. These groups include at least one species (*Pagrus ehrenbergi*) previously included in the supra-thermocline sparid subcommunity, together with a number of ecologically similar forms (*Pagellus*, *Priacanthus*, *Dactylopterus*, and *Epinephalus*) and at least one (*Raja miraletus*) that was previously unallocated because it was considered a eurybathic species. In both cruises, these groups occurred rather frequently on hard deposits, and we now believe that these are the species which represent the element of the sparid complex that is able to penetrate above the thermocline onto sandy or broken corally deposits avoided by the sciaenid community. The evidence further suggests that even below the thermocline these species tend to occur together.

In the data from each cruise, there was a remarkably stable group (20) associated with the groups discussed above, composed of three species of semipelagic taxa: *Boops boops*, *Scomber japonicus*, and *Trachurus* spp. These are cold-water species which in the Canary and Benguela Current form surface shoals and which in the tropical Gulf of Guinea occur only in a rather narrow depth and temperature range and are most abundant near the bottom of the thermocline at about 17 C. The degree of association observed suggests that they form mixed shoals.

Groups 8 and 9 of both GI and GII extend deeper and occur more frequently on soft deposits than the other groups put in assemblage D and it is these which form the typical subthermocline sparid community, dominated by species of *Dantex*, *Lepidotrigla*, *Paracubiceps*, *Uranoscopus*, and *Pentheroscion mbizi*.

The deep shelf community (E) was identifiable as group 10 of both GI and GII, and the environmental properties showed that it was restricted to depths of around 200 m and to temperatures below 15 C. There was a rather large gap in sampling between 200 and 400 m on each transect and somewhere between these two depths the fauna changed completely to that represented by groups 11 and 12, and 11 and 21 of GI and GII, respectively. This continental slope community (F) occurred at temperatures between 7 and 10 C. In earlier studies it was recognized only by Salzen (1957). As might have been expected, this poorly known slope community was not consistently represented in the analyses of the data from the two surveys and was shown to include some ecologically based diversification. In Fig. 3 the GII data demonstrated that the species of group 21 *Hypoclydonia bella* and *Chascanopsetta lugubris*) were included in the assemblage of species-groups co-occurring on some transects where sandy and stony substrata dominated. Their co-occurrence with group 11 in some trawl hauls, however, suggests that group 21 may represent the fauna on patches of sandy deposit in regions of a mosaic of sandy and muddy substrata on the upper parts of the continental slope.

FACTORS INFLUENCING THE DISTRIBUTION OF GROUPS

The depth distribution of each group was examined (Table III) by coding the depths (0 = 15–20 m, 1 = 30 m, 2 = 40 m, . . .), calculating the mean coded depth of occurrence and then comparing the observed distribution of coded depths of occurrence for the groups with that expected for a Poisson distribution with this mean. For the shallow-water groups in both seasons (1–7, 13–18; both GI and GII), none of the observed distributions were significantly different from expectation (all $p \geq 0.10$, Kolmogorov–Smirnov goodness-of-fit test; Tate and Clelland, 1957). This finding indicates that these groups were not distributed evenly in the upper 70–100 m but that each had a favored depth, above and below which it occurred randomly; these groups showed the same sort of distribution of depth that one would expect from an underwater vehicle trying to maintain a certain depth but subject to random error in measurement of, or adjustment to, depth.

The information on the groups in deeper water is not strictly comparable because of the wider spacing of the deeper trawl hauls. With this limitation, the data suggest that some deeper groups were not randomly distributed with depth; the observed distributions generally were either sharply truncated upwards or limited to a single depth among those fished.

By and large, comparable groups in the two survey periods occupied similar depth ranges and, as temperature generally followed depth directly, experienced similar temperature regimes. The greater median depths observed in GII for a few groups (1, 2, 5, and 8) provide slight evidence that they, or at least some of their members, moved into slightly deeper water in the warmer season; these groups were all members either of the sciaenid community or of that element of the sparid community living on muddy ground below the thermocline. No group typical of sandy or rocky substrates showed changes in its median depth range between the two cruises; this is probably an expression of the depth restriction of the hard sandy and stony deposits over most of the survey areas. It is also possible, of course, that this is related to the fact that the depths of occurrence of shallow-water groups, principally on sandy bottoms (groups 13–18; median depths, 30–40 m), were significantly greater ($p < 0.05$, Mann-Whitney U test; Tate and Clelland, 1957) than those for the groups typical of muddy bottoms (groups 1–7; median depths, 20–40 m). Perhaps those species that prefer shallow water over mud and sandy mud move inshore or offshore in response to seasonal changes in the environment, whereas those usually found over sand or rock do not undertake such movements because they live deeper where seasonal effects are less.

The frequencies of occurrence of five types of bottom deposit — mud, sandy mud and muddy sand, sand, sand and gravel or rocks, and rocks or coral — were tabulated for all stations. The distributions of observed frequencies of occurrences of the species groups at stations representing each major type of bottom deposit were compared with the distribution expected on the hypothesis of independent distribution of groups and bottom deposit types (K–S test; Tate and Clelland, 1957). There was a clear separation of the species groups into two assemblages corresponding to those based on joint occurrences of transects (Table III); one assemblage tended to occur more frequently than expected over mud and sandy mud substrates, and the other over sand and rocks. In their relation to substrate type, the groups in the second assemblage showed, proportionately, a greater number of biased distributions (at <0.10) than those in the first assemblage.

To consider geographic distribution of the species groups, the GTS area was subdivided; transects at which any group either began or ended a continuous distribution (present on three or more contiguous transects) were tabulated and those transects with the largest numbers of either terminations or starts were chosen to form six geographical subregions between Cape Roxo and the Congo River, with boundaries near Freetown, Cape Three Points, Cotonou, Douala, and Cape Lopez (Fig. 1, Table III). The frequencies of occurrences of the species groups in these six regions were compared with those expected on the hypothesis of equal probability of occurrence on all transects (K–S test; Tate and Clelland, 1957); this showed (Table III) that the groups and assemblages typical of muddy deposits were found more frequently than expected by chance in the three regions from Cotonou eastwards (D, E, F), and those typical of sandy substrata, though they did not as often show biased distributions (at $p < 0.10$), tended to be more frequent west of Cotonou (A, B, C).

This apparent difference in distribution was probably mostly related to the distribution of sediment types; for example, 83% of all stations with sand or rock bottom were in regions A–C. It cannot be attributed to the distribution of bottom types entirely, however, because only slightly over half (56%) of the stations with mud or muddy sand were in regions D–F. Furthermore, on the assumption that D, E, and F were equally likely to be occupied by groups preferring mud and A, B, and C by those preferring sand, significantly too many groups favored region D and too few favored region B.

CONCLUSIONS

The analysis presented and discussed here has confirmed in an objective manner the reality of the communities of demersal fish whose existence on the West African continental shelf had been previously postulated independently by a number of observers from their subjective treatment of trawling survey data. This agreement not only increases the reliance which may be placed upon this objective method of analysis of recurrent species groups, previously tested on zooplankton (Fager and McGowan, 1963; Sheard, 1965), but also confirms the likelihood that subjective judgments of the sort also being considered here may, in fact, be valid and useful; they should not be neglected in fishery exploration when more refined methods cannot be applied to the data.

One of us (Longhurst, 1967) has suggested that a search of the literature on trawling surveys in all parts of the tropical oceans has produced data which may subjectively be arranged to indicate that species assemblages analogous to those whose occurrence in the eastern Atlantic is here confirmed may also occur throughout the tropical Atlantic and Indo-Pacific, at least in environment similar to those in the Gulf of Guinea.

This computer analysis, by confirming the reality of these communities in one part of the tropical ocean, lends weight to the supposition that demersal fish communities on level sea bottoms on the tropical continental shelf, may generally, or at least frequently, be organized in a rather simple fashion similar to that described here.

ACKNOWLEDGMENTS

This work was supported in part by the National Science Foundation (Grant G-7141, GS-5800); in part by the Marine Life Research Program (Scripps Institution component of California Cooperative Oceanic Fisheries Investigation, sponsored by the Marine Research Committee of California); and in part by the Bureau of Commercial Fisheries of the U.S. Fish and Wildlife Service (contract 14-17-0007-139, 221 with Scripps Tuna Oceanography Research Program).

The authors also wish to acknowledge the help of Dr F. Williams, Director of the Guinean Trawling Survey, and the Organization of African Unity, for supplying the data on which the study was based.

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Minchinia nelsoni (Haplosporida) Disease Syndrome in the American Oyster *Crassostrea virginica*

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SYNOPSIS. *Minchinia nelsoni* disease was studied in 3 populations of oysters from Marumsco Bar, Pocomoke Sound, Maryland. The native population was sampled regularly beginning in 1961 shortly after the disease invaded this area. Two populations of healthy year-old oysters were introduced (one in 1965 and one in 1966) into Pocomoke Sound and studied concurrently with the native population to determine the course of development of the disease and epizootic differences in populations.

Gross and microscopic examination of oysters showed progressive stages of infection. *Initial infection* occurred in epithelia of the filtering organs (gill, palp, water tubes) and spread into connective tissue where hyaline hemocytes infiltrated. *Intermediate infection* was characterized by local infection and infiltration of connective tissue in and adjacent to epithelia of gill, palp, esophagus, stomach, gut, diverticula, and gonadal alveoli. *Advanced infection* was recognized by the general invasion and infiltration of connective tissue and the circulatory system by hyaline hemocytes. *Terminal infections* showed histologically massive pyknosis of nuclei and necrosis of tissues before outward signs of death were apparent. *Remission* of the disease was recognized by diminution of infection intensity and infiltration; localization of parasites near external epithelia; increased pigment cell formation; and diapedesis and deposition of necrotic parasites and tissue against the shell, followed by external conchiolinous encapsulation.

Death from *M. nelsoni* disease may be attributed in part to seasonal environmental or physiologic stresses, which infected oysters, weakened and in poor condition due to the pathologic manifestations of the disease, are unable to tolerate. The gross pathologic signs of disease were: pale digestive gland, poor condition, mantle recession, weakness, and conchiolinous shell depositions. The microscopic signs were: diapedesis, relative decrease in numbers of phagocytes; relative increase in numbers of hyaline hemocytes; phagocytosis, fibrosis, cellular infiltration, abscess, ulceration, excessive pigment cell formation, mechanical disruption, pyknosis, and necrosis.

A HAPLOSPORIDAN parasite, originally designated "MSX" (33, 46) and later named *Minchinia nelsoni* (36), has caused extensive oyster mortalities along the mid-Atlantic coast of the United States (2, 3, 4, 8, 17, 34, 35). Sporulating stages of *M. nelsoni* have been described (13) and a tentative life cycle proposed (20). Few reports (50, 69, 70, 71) have dealt with the pathology of any haplosporidan infections in oysters.

The purpose of this report is to provide information about the syndrome of *M. nelsoni* disease in the oyster and to show how it relates to other oyster disease processes. Progressive stages of infection by *M. nelsoni* have been recognized, starting with initial infection and leading to either death or recovery depending on environmental, genetic, or physiologic influences. Thirty-one specific disease signs and responses in oysters have been described in the literature, 22 of which appear to be associated with *M. nelsoni* infection. In this paper 8 gross signs of disease are described from oysters with *M. nelsoni* infection.

MATERIALS AND METHODS

Sampling. Oysters were dredged from Marumsco and Kitts Creek oyster beds, 2 areas about 1 mile apart in Pocomoke Sound, Chesapeake Bay, Maryland. Samples of 25 or 50 oysters were obtained weekly, semi-monthly, or monthly from April 1961 to December 1967. *M. nelsoni* 1st appeared in Marumsco oysters in the fall of 1960 (8) and reached epizootic proportions (32% prevalence) in September 1963. Uninfected 1-year-old oysters planted on Kitts Creek Bar in April 1965 and on Marumsco Bar in May 1966 were sampled concurrently with the native population. Introduced oysters could be readily distinguished by the number of seed oysters per shell. The setting intensity for Pocomoke Sound was extremely low during this study while the area from which these seed oysters came was high, resulting in 5-10 oysters per shell. Shells containing less than 5 oysters were arbitrarily assumed to be natives and were not used. Samples of the native population were collected from unseeded areas. About 5,000 individual oysters have been examined during this investigation. Data on salinity, temperature, water depth and substrate were recorded with each sample collected.

Laboratory procedures. Samples were brought to the laboratory within 4 hours and refrigerated at 5 C (usually overnight but occasionally up to 4 days) until processed and examined.

After each oyster was assigned a number and measured, it was opened at the hinge and the adductor muscle carefully severed to remove the right (upper) valve. Each oyster's condition was rated as fat, medium, or watery. Abnormalities of color, tissue, and shell were recorded for each specimen. Oysters were then removed from the left (lower) valve and cross-sections of tissue approximately 6 mm thick were cut from the visceral mass. Sections of the palp region were placed in individual coded jars with seawater for microscopic examination *in vivo*. Cross-sections of tissue from the visceral mass were fixed immediately in Davidson's fixative (62) for histologic processing. The rectum was removed from each oyster and cultured in thioglycollate medium (59) for the diagnosis of *Dermocystidium marinum*. Since oysters with pale digestive diverticula often were diseased (13, 15, 74), this condition was recorded for samples taken after January 1965. Fresh tissue squashes were made by placing a small portion of the visceral mass on a slide with seawater and mashing it with a cover glass to a layer about one or two cells thick. Squashes were examined microscopically for parasites and cellular response of the host. The entire tissue area was also examined routinely for necrosis, large parasites, spores, and pigment cells. Thickness of the tissue masked cellular response and small parasites; therefore the peripheral region of the tissue, where cells tended to form a unicellular layer, received special attention.

Fixed tissues were embedded, sectioned at 6 μ, and stained with Ziehl's fuchsin-Harris' hematoxylin-eosin (18). Stained sections were examined for parasites, pathology, and cellular responses.

OBSERVATIONS ON UNINFECTED OYSTERS

Oysters have an annual cycle in which condition, indicative of the amount of glycogen stored in the tissue (30), increases and decreases seasonally. Most oysters from healthy populations have the same gross appearance and condition. Oysters normally reach their peak of condition in the fall and winter, when they appear "fat." Their color

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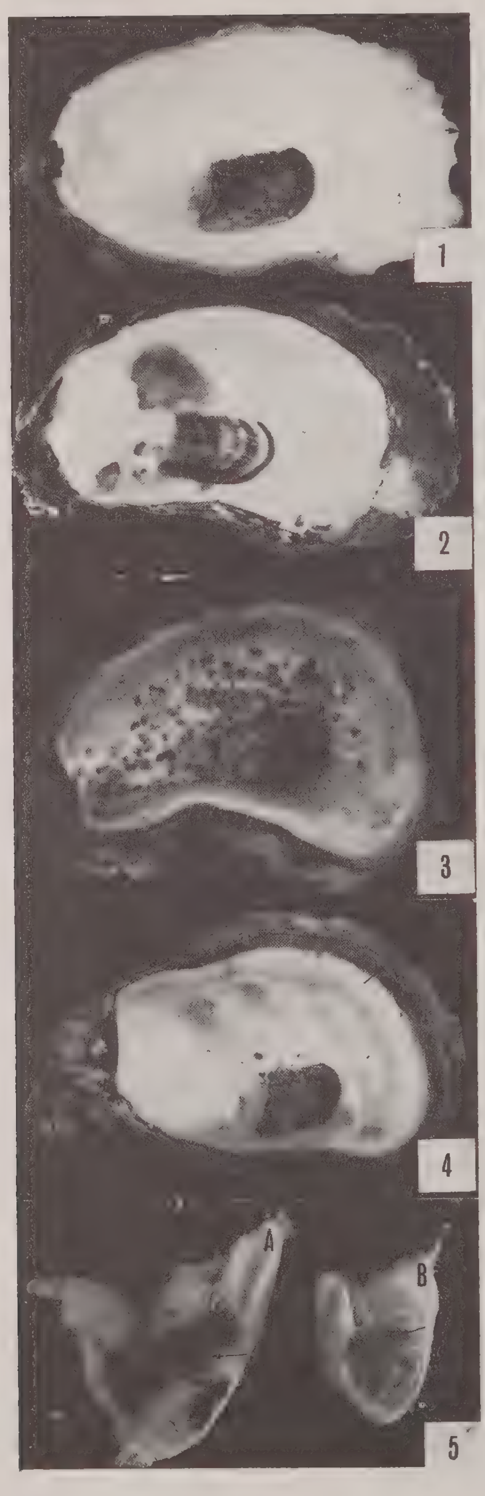


Fig. 1. Shell of healthy oyster; note clean shell margin. Fig. 2. Shell of infected oyster. Heavy fouling of the shell margin indicates prolonged mantle recession. Fig. 3. Shell of infected oyster with indication of mantle recession and many conchiolinous deposits (arrow). Fig. 4. Shell of oyster in the process of overlaying fouled margin with new conchiolin periostracum. Fig. 5. Cross sections thru the visceral mass of oysters taken during the active feeding season. A. healthy oyster; note dark appearance of digestive diverticula. B. heavily infected oyster; note comparatively pale appearance of digestive diverticula.

is creamy-white and the body is firm, filling the shell cavity. Oysters normally appear "watery" in spring and in early summer after spawning, indicating poor condition; they have translucent mantles and flaccid tissues and often appear emaciated. Oysters develop creamy-appearing gonads in the spring. "Medium" oysters, common in the early fall, have characteristics transitional between "watery" and "fat".

Uninfected oysters have sharp distal shell edges. After removal of the right valve, the nacreous surface of the left valve appears clean and white to the edge of the shell, where a thin margin of conchiolin begins (Fig. 1). The edges are often broken off in dredged oysters. The digestive diverticula are brown to dark brown (Fig. 5A).

Fresh squashes of uninfected oysters examined microscopically have no generalized concentration of hemocytes and appear uncluttered with cells. The diverticulum pigment is usually bright yellow and small globules of glycogen are prominent in squashes of "medium" and "fat" oysters. The most common hemocyte is a large (15-30 μ) granular amoeboid phagocyte (Fig. 6) which often occurs in dense masses (Fig. 9). A less abundant type of hemocyte in healthy oysters is a small (8 μ), non-granular, hyaline, lymphocytoid form with a large (5 μ) nucleus (Fig. 7). These cells are referred to here as hyaline hemocytes to distinguish them from the large phagocytes. These 2 types of hemocytes are the most common in the oyster (31, 73, 77, 78, 83), and altho other types may occur they are possibly either transitional or degenerate. Pigment cells (Fig. 8) (10, 32, 43, 75) are always present in low concentrations in normal tissue, and contain yellow granules of varying sizes.

Connective tissue in sections of uninfected oysters appeared as a light area of large interconnecting cells with small nuclei (Fig. 18). Localized concentrations of phagocytes are often found near the gut, stomach, and digestive diverticula (Fig. 19). Phagocytes (Fig. 12) are 10-12 μ in diameter and contain small (2-3 μ) nuclei with eccentric nucleoli and a network of chromatin. The cytoplasm often forms lobed pseudopodial protrusions, but most cells appear spherical. Cytoplasmic granules, prominent in live phagocytes, were lost during histologic processing. Hyaline hemocytes (Fig. 14), uncommon in uninfected oysters, are spherical, about 8 μ in diameter and contain nuclei similar to those in phagocytes, but generally larger (4-5 μ). Granules within pigment cells (Fig. 16) remain yellow after staining or occasionally have varying degrees of acid-fastness.

TABLE 1. *Effect of* M. nelsoni *infection on gross appearance of oysters introduced in Pocomoke Sound, Maryland in 1965 and 1966.*

Sign	Uninfected		Infected		Percentage of oysters showing sign that were infected	Sample series
	Number examined	Percentage showing sign	Number examined	Percentage showing sign		
Mantle recession	249	1.6	101	34.6	89.7	1
Mantle recession	120	0.8	30	50.0	93.8	2
Condition						
Fat	109	43.8	19	19.8		1
Medium	121	48.7	45	44.8		1
Watery	19	7.6	37	36.6		1
Pale diverticula	120	3.3	30	56.6	81.0	2

Samples in series 1 were collected monthly for 1 year from the population introduced in 1965; samples in series 2 were collected monthly for 6 months from the population introduced in 1966.

PATHOLOGY OF *M. nelsoni DISEASE*

Gross and microscopic. The most apparent signs of disease occurred as shell abnormalities. Most of the heavily infected oysters had "mantle recession" leaving the marginal area of the shell exposed to fouling organisms. The unprotected area became heavily fouled with sedentary organisms, and a wide (2-10 mm) band of fouling developed along the inner margin of the left shell (Fig. 2). Ninety-one percent of introduced oysters with mantle recession were infected (Table 1).

Oysters with raised yellow-brown conchiolin deposits on the nacreous surface of the shell (Fig. 3) were found in old surviving populations which had remained in enzootic areas for several years. These deposits contained a creamy yellow fluid which consisted of moribund *M. nelsoni* plasmodia, hemocytes, and cellular debris. Only a small percentage of oysters had this condition, but when present it was a reliable gross indication of the disease.

A 3-year period of high prevalences of infection, mortality, and mantle recession in the native population was followed by a marked reduction of these phenomena. Many oysters with evidence of previous mantle recession were apparently in the process of overlaying the fouled inner shell margins with new periostracum (Fig. 4).

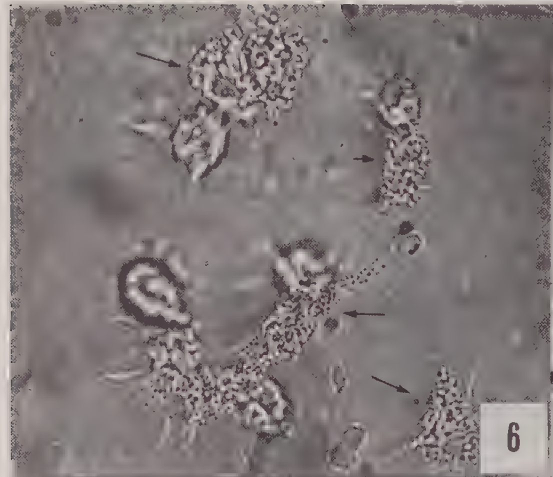
Infected oysters were usually in poorer condition than uninfected oysters (Table 1). Those rated as "fat" were rarely infected and when they were found, the disease was invariably in either early developmental or arrested stages. Sixty-six percent of the "watery" oysters were infected, but other factors such as heavy *Polydora* or *Cliona* infestations also tended to accompany "watery" condition.

Comparatively pale (yellow, tan, or white as opposed to brown or dark-brown) diverticulum hues were recorded; Table 1 indicates the close relationship between digestive gland color (Fig. 5B) and infection. Eighty-one percent of the oysters with pale digestive glands were infected. All oysters from disease enzootic areas which had mantle recession, "watery" condition, and pale digestive diverticula (and the majority of oysters which had any 2 of these characteristics) had extensive *M. nelsoni* infection. Another method of detecting diseased oysters was reported by Andrews (4). He weighed under-water oysters weekly and found that failure to gain weight was a diagnostic criterion of disease.

Large numbers of hyaline hemocytes (Fig. 7) were evident in tissue squashes of moderately and heavily infected oysters. Phagocytes (Fig. 6), abundant in healthy oysters, were uncommon in infected oysters. The relative abundance of these 2 cell types (Fig. 9 uninfected, Fig. 10 infected) provided for tentative diagnosis on the basis of cellular response alone. Oysters with recently acquired infections usually required histologic examination for accurate diagnosis. Surviving oysters from native populations were often lightly infected, had little cellular infilration of the vesicular connective tissue, and had excessive numbers of pigment cells (Fig. 11). Infections were more difficult to confirm in this population than in the introduced population regardless of the technic used.

Histopathology. The portal of entry of *M. nelsoni* in the oyster is the epithelial lining of the gill and inner palp (4, 35, 50). Plasmodia are localized within epithelia and restricted by basement membranes (Fig. 13). Clear vacuoles were evident around many plasmodia, but may not indicate lysis, since clear areas may be found in uninfected epithelia and might be attributed to fixation. Proliferation of the parasite began at the invasion site and continued as the disease advanced. An intense cellular reponse characterized by infiltration of the affected tissue by hyaline hemocytes (Fig. 14) occurred when the parasites invaded the connective tissues and circulatory systems. Immediately preceding mortality, pyknosis and necrosis (Fig. 15) of host and parasite cells were common. Localized abscesses (Fig. 17) containing fibroblasts, hemocytes, and moribund *M. nelsoni* plasmodia were found in connective tissue adjacent to the mantle in oysters with newly formed conchiolinous shell deposits (Fig. 3).

Early infections were usually localized in one epithelium of either the palp, gill, or water tubes (50). Figure 20 shows this type of infection in the palp. The upper epithelium (Fig. 20A) was heavily infected, whereas the lower epithelium (Fig. 20B) was healthy. Heavily infected gill epithelia are often seen in the process of sloughing (35, 50), possibly from mechanical disruption by massive numbers of parasites. Secondary invasion apparently occurs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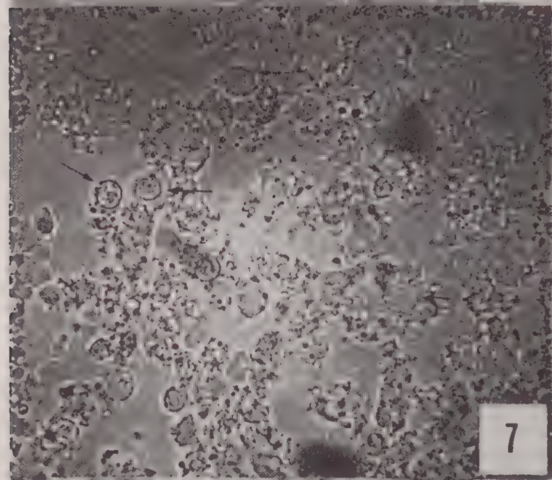
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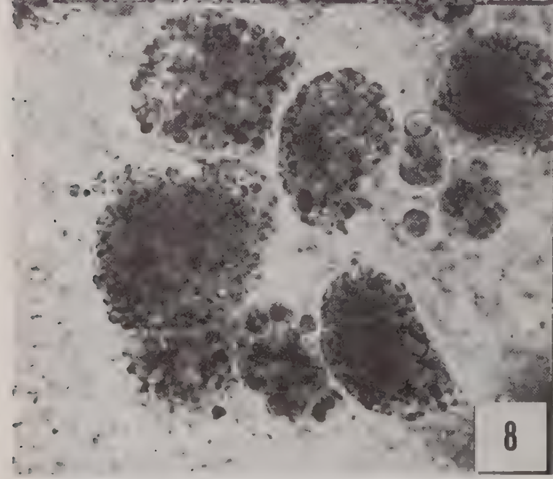
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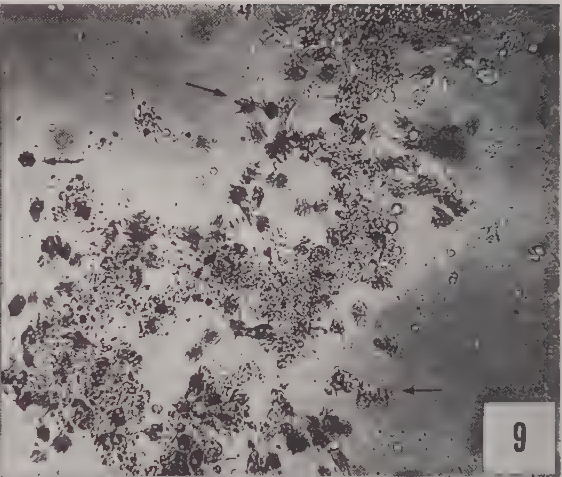
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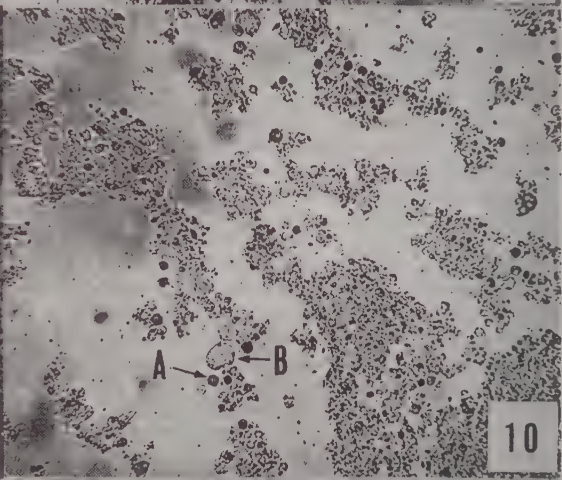
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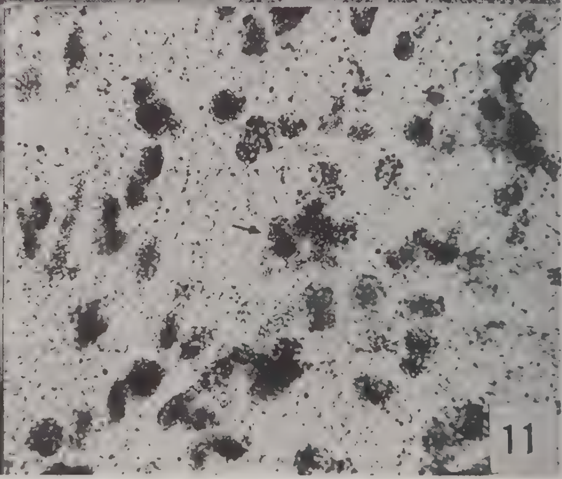
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further along the alimentary canal from parasites released in sloughed tissue and carried along by ciliary action. Infection of the hemolymph spaces and connective tissue elicits an extensive cellular response in the affected areas characterized by infiltration of hyaline hemocytes (Fig. 21). The condition is easily distinguished from concentrations of normal phagocytes (Fig. 19) by its dense appearance, an effect produced by the volume ratio of nucleus to cytoplasm in the 2 cell types. Because of their smaller size, many more hyaline hemoctyes than phagocytes can occupy a given area. Infections progress to a stage where the connective tissue has characteristic massive infiltration accompanied by intensive parasitic infection. The ducts and tubules of the digestive diverticula, which normally are composed primarily of tall columnar epithelial cells (Fig. 19), often appeared flattened and contracted (Fig. 22). General necrosis of host tissue and parasites was evident in dead and dying oysters (Fig. 22). Infected oysters from the native population which had survived several annual mortality periods, and infected oysters from low salinity environments, often had very heavy concentrations of pigment cells (Fig. 23).

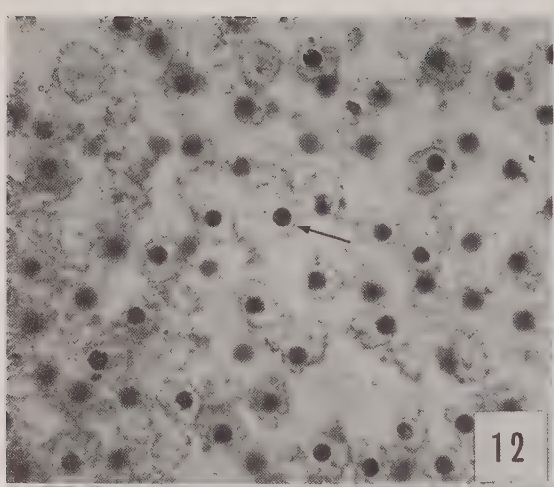
Photomacrographs 24 thru 32 show various types of infections found in this study. The gill and connective tissues appear uncongested in normal oysters (Fig. 24) and the gonad is well-developed in appropriate seasons. After generalized infection of the gill, heavy congestion appears in the affected tissue (Fig. 25, arrow). In Fig. 26 the infected tissue is characterized by congestion in one palp (A), one gill lamella (B), and one region of the gonad (C). The remaining tissues appear normal. Extensive destruction of gametic tissue by *M. nelsoni* was seen microscopically. In Fig. 27 the infected area and congestion is localized in one region of the gonad (A) and around part of the stomach epithelium (B). An extensive area of involvement is seen in Fig. 28; congestion is present in the gonad (A), the stomach (B), the gut (C), the diverticula (D), and the hemolymph sinuses (E). Heavily infected oysters (Fig. 29) have massive congestion of all tissues. In dead or dying oysters, all tisues show necrosis and a slight decrease in congestion (Fig. 30). Oysters from the surviving population usually are very lightly infected thruout the tissue and often have gonadal development (Fig. 31A), little congestion, and large numbers of pigment cells (Fig. 31B). Figure 32 is a section from an oyster with conchiolinous shell deposits (Fig. 3). The gonad contains developing sperm (A); massive numbers of pigment cells are evident in the connective tissue, and congestion and localized abscesses adjacent to the mantle (B) contain moribund *M. nelsoni* plasmodia. Other tissues are uninfected and appear normal.

Stages of infection. As a result of this study progressive stages of infection can be defined in 5 categories—initial, intermediate, advanced, terminal and remission.

Initial infections are defined as those infections restricted to the filtering organs of the oyster. Other investigators (4, 50) have indicated that oysters acquire infection in the warm season of the year, when localized infections in gills and palps are most common. Infections apparently originate in the epithelia (4, 19, 20, 35, 50). Some sections have light infections (1-10 plasmodia) in a small area of one epithelium. These plasmodia, usually actively proliferating (20), are rarely observed as uninucleate forms, and seldom contain more than 10 nuclei—indicating a young stage of the parasite. Other infections are characterized by acute localized invasion of one gill lamella suggesting that only one infective particle is necessary to establish the disease and that the disease spreads more rapidly in the direction of water flow (50). Widespread invasion of only the gill tissues (Fig. 25) might suggest an abundance of infective particles, but more probably it represents further progress of the disease because: (1) deeper tissue penetration invariably accompanies this type of invasion; (2) multiple foci of infection, restricted to epithelia of the filtering organs, have not been seen; and (3) an abundance of uninucleate amoebulae or spores (logical infective agents of *M. nelsoni*) have not been found in initial infections. The nature of initial infection, as defined, supports other hypotheses (4, 50, 71) that the infective agent is waterborn.

Intermediate infections show local invasion of the connective tissue and epithelia of the visceral mass, accompanied by infiltration of the affected areas by hyaline hemocytes. The infiltration appears to be a defense mechanism which temporarily impedes dissemination thru the circulatory system, and is less effective in other areas, such as the gonad, which are unrestricted by interlocking vesicular connective tissue cells. The evidence for method of invasion comes from the common occurrence of local congestion in the connective tissue adjacent to epithelia of the digestive tract, and in the alveoli of the gonad (Figs. 26, 27, 28). Sloughing of gill and palp epithelia, also observed by Myhre (50) and Haskin, Canzonier and Myhre (35), releases parasites which are apparently carried down the digestive tract, perhaps causing secondary infection of the epithelia of the esophagus, stomach, diverticula, and gut—often before extensive invasion of the circulatory system occurs (Figs. 27, 28). The rarity of local infections in the digestive tract without accompanying infection of the filtering organs or gonad indicates that the digestive tract is not an important site for initial infection. Initial and intermediate infections were common in oysters longer than 8 cm. The first indication of infection in small oysters (less than 8 cm), sampled monthly, was a general systemic invasion 3 months after introduction, which indicates that the disease spreads rapidly thru tissues. More frequent

Figs. 6-11. *In vivo* photomicrographs. Fig. 6. Phagocytes from healthy oysters; note granules and pseudopodia. × 1000. Fig. 7. Hyaline hemocytes from infected oyster; note small size in relation to phagocytes, large nuclei, lack of granules, and spherical shapes. × 1000. Fig. 8. Pigment cells; note irregular shaped granules of various sizes. × 1000. Fig. 9. Phagocytes from healthy oyster 25 second exposure; blurred appearance of cells reveals the highly motile character of these cells. × 250. Fig. 10. Hyaline hemocytes from infected oyster, 25 second exposure; note lack of motility. × 250. A. Individual hyaline hemocyte. B. Plasmodium of *M. nelsoni*. Fig. 11. Pigment cells in recovering oyster; note large concentration of cells. × 250.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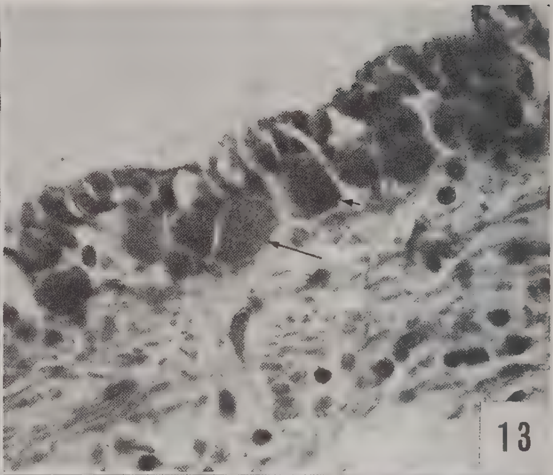
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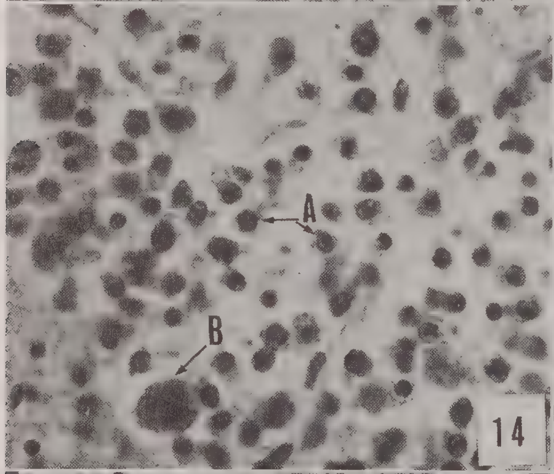
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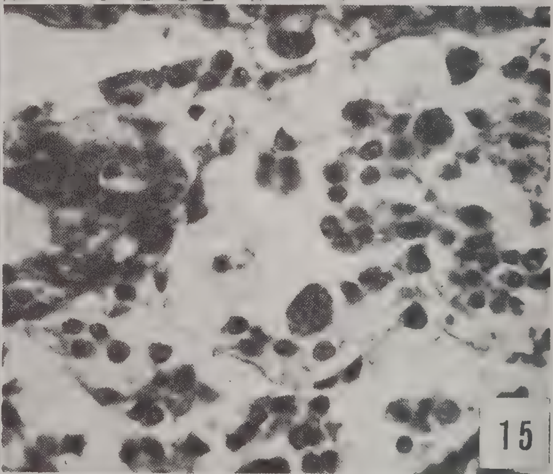
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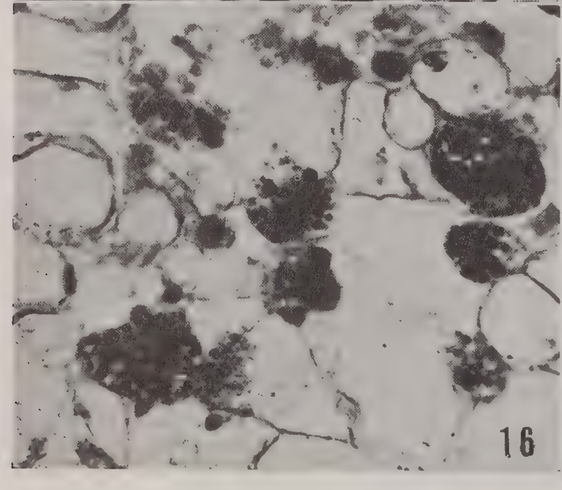
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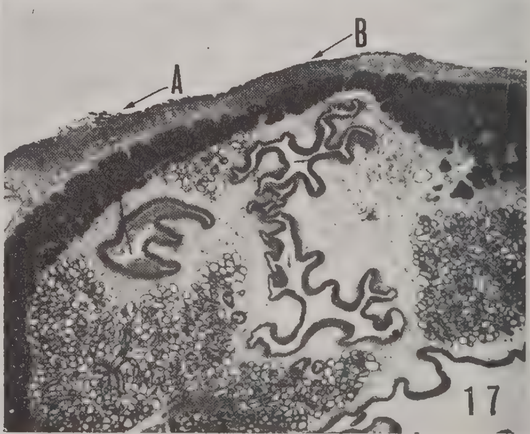
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sampling would be necessary to reveal disease progression in smaller oysters.

Advanced infections are characterized by massive parasitic invasion and infiltration by hyaline hemocytes of the vesicular connective tissue and dissemination thru the hemolymph system. Plasmodia are not usually found in epithelia except during sporogony (13, 20). Often, the epithelia of the digestive diverticula appears flattened or contracted, with cilia either degenerative of absent. Oysters with advanced infection usually have pale digestive glands (Fig. 5B), are in poor condition, and often have signs of mantle recession (Fig. 2). Mantle recession appears about 3 months after introduced populations 1st show infection. The normal appearance of the epithelia of the gill and palp in oysters with advanced infections indicates that oysters are able to repair tissues damaged in the earlier stages of the disease and that mechanical disruption is not a direct factor of death.

Terminal infection, recognized histologically by the occurrence of necrosis and pyknosis of host and parasite cells, is common immediately preceding and during mortality periods, frequently before gross signs of death are evident. The 1st gross sign of death is weakness of the adductor muscle, detected by the ease with which the valve can be moved. Weak oysters, when stored out of water, also have a tendency to lose mantle fluid and, when tapped with a hard object, sound hollow. Oystermen in the United States refer to them as "cluckers" and those in England as "hocklers" (53).

Remission. Remission is characterized by: (1) abatement of cellular infiltration in tissues; (2) occurrence of large numbers of pigment cells in the vesicular connective tissue; (3) inactive, moribund-appearing parasites (cystoid and abortive sporogonic stages) (20); (4) phagocytosis of parasites; (5) decrease in numbers of parasites; (6) localization of parasites in and near epithelia—especially of the gut, stomach, and mantle; (7) occurrence of parasites and phagocytes in the lumens of the stomach and gut; and (8) progressively lower prevalence and intensity of infection in populations without noticeable mortality. Items 4, 5, 6 and 8 support the experimental studies of others (5, 6, 22, 23, 26, 72, 80, 81, 82) and indicate that phagocytosis and diapedesis are, under certain conditions, defense mechanisms against naturally occurring disease. I have observed phagocytosis and cellular exudation *in vivo*. Oysters were exuding from their gill tissues a creamy mucoid substance which contained phagocytized and free *M. nelsoni* plasmodia. A similar cellular exudate, occurring as rejecta, appeared in a healthy oyster about 1/2-hour after pericardial injection of tissue containing *M. nelsoni* plasmodia.

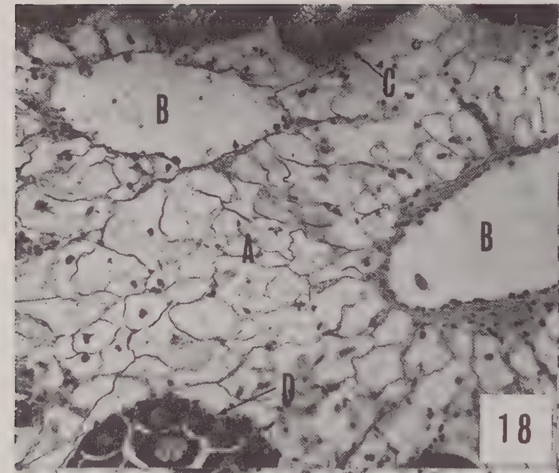
Massive increases in parasite prevalence have been noted on several occasions following remission, with the return of higher water temperature and salinity. Infections are characterized by heavily infiltrated lesions containing proliferating parasites, localized near internal epithelia and hemolymph vessels. This type of intermediate infection might represent a relapse of the disease due to the return of favorable conditions for the parasite, in oysters which had previously undergone remission.

Remission from *M. nelsoni* infection may in some instances be caused by resistance or immunity. The native population from Marumsco Bar, after 5 years of exposure, consistently had a much lower prevalence of infection thruout the year than introduced populations concurrently sampled after less than 2 years of exposure. Oysters from the old native population with the characteristics of remission described earlier, often had new periostracum overlaying previously fouled shell margins (Fig. 4); however, systemic infections of *M. nelsoni* often could not be diagnosed. The usually good condition of these oysters indicates complete recovery from the disease. Oysters with conchiolin shell deposits (Fig. 3) and localized lesions near the mantle (Fig. 32) are found in populations which have been exposed to the disease 1.5 years or more. The healthy appearance of the rest of the tissues in these oysters and the difficulty in positively diagnosing *M. nelsoni* in oysters with old calcified shell deposits, indicate that these oysters were in the process of recovering from the disease. Old oysters from the native population with signs of previous infection (mantle recession, massive numbers of pigment cells) have been found with localized gill infections, indicating that reinfection may occur. Parasites appear moribund in most cases of this kind and little infiltration is evident; it is doubtful, therefore, whether reinfections progress beyond the initial sites of infection. The rarity of signs of remission in the introduced populations indicates that resistance to the disease becomes apparent gradually in the population after repeated exposures. The occurrence of apparently abortive reinfections, the obvious recovery of certain oysters, and low prevalence in the native populations suggest "acquired immunity." It is still too early to determine whether genetic immunity similar to that described for Malpeque Bay oysters (41, 42) has developed, but no obvious differences in disease prevalence are apparent in small oysters from the native population in comparison with older native oysters.

A REVIEW OF OYSTER DISEASES AND THEIR MANIFESTATIONS

Many research papers have been published in this century which dealt with oyster diseases and parasites and experimental pathology in which normal oysters were used. Apparent problems in terminology exist because of loose adaptation of vertebrate terms to describe invertebrate cell types and responses. Consequently whenever possible, at-

Figs. 12-17. Stained sections. Fig. 12. Phagocytes in hemolymph sinus of healthy oyster; note pseudopodial projections, size of nucleus, and absence of granules. × 1000. Fig. 13. Initial infection in palp epithelium; arrows point to 2 of several *M. nelsoni* plasmodia in epithelium. × 1000. Fig. 14. Hyaline hemocytes in advanced infections; note A, large nuclei and limited cytoplasm of hemocytes, B, *M. nelsoni* plasmodium. × 1000. Fig. 15. Pyknosis and necrosis of host and parasite cells in dying oyster. × 1000. Fig. 16. Pigment cells in connective tissue. × 1000. Fig. 17. Localized lesions adjacent to mantle in recovering oyster. A. ulcerated abscess. B. intact abscess. (These lesions were adjacent to conchiolinous shell deposits shown in Fig. 3.)



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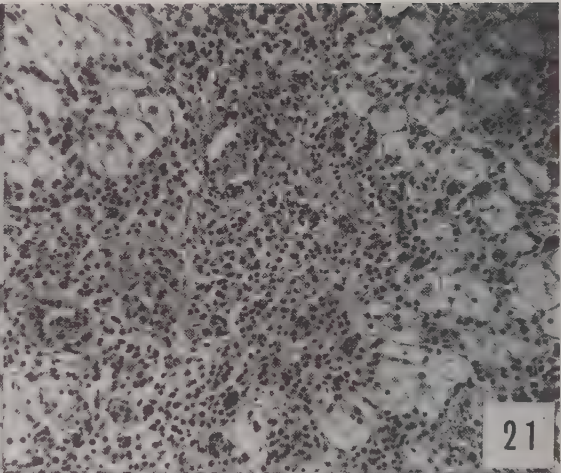

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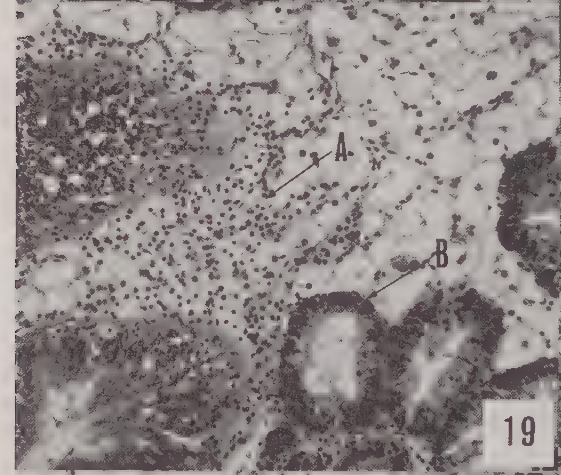

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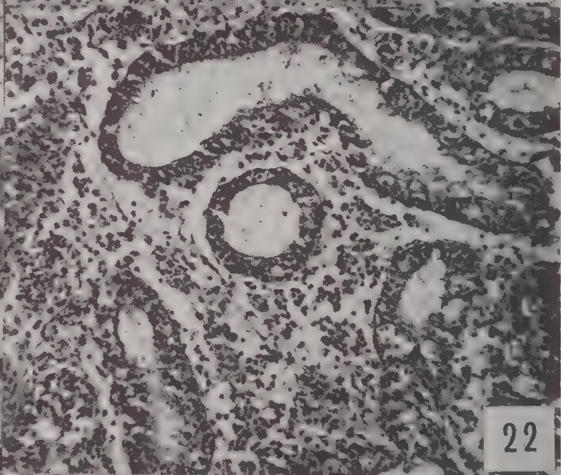

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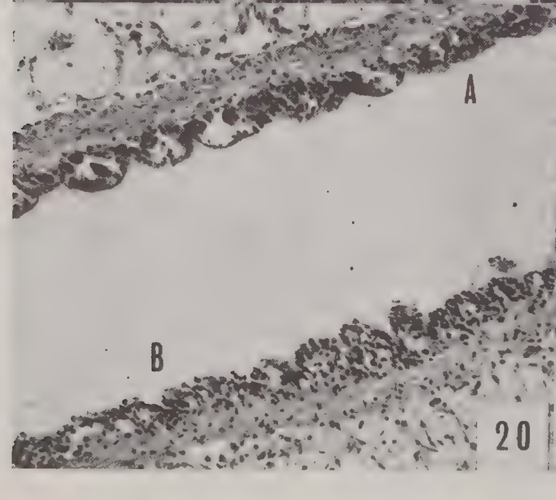

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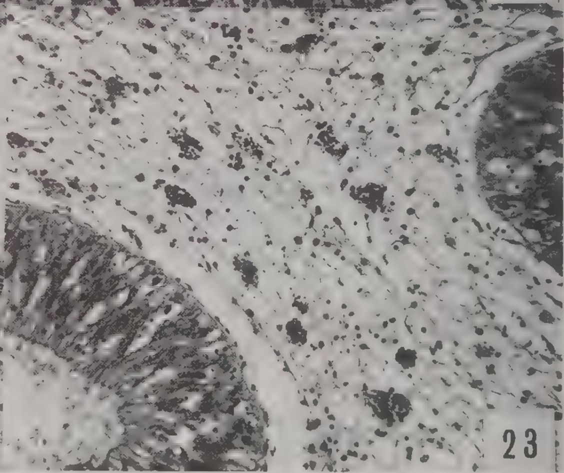

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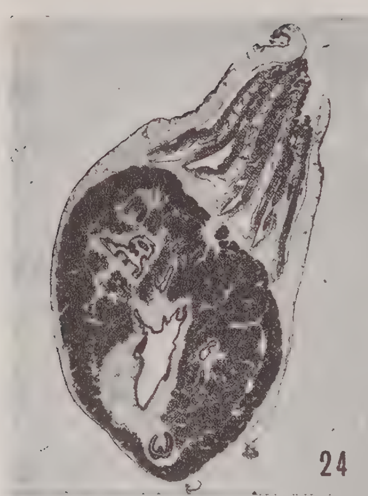
tempts will be made to clarify terms. Previously described disease manifestations of oysters will be integrated to indicate patterns of oyster disease pathology with particular reference to *M. nelsoni* disease. *Previous studies.* Earlier studies of other oyster diseases have included some consideration of pathologic manifestations. Orton's detailed account of mortality in *Ostrea edulis* in England (53) described many of the general signs and pathologic processes involved in oyster diseases. Roughley (60) found many of the same signs associated with mortality in Australian mud oysters *Ostrea cucculata*. Needler and Logie (52) and Logie (41) studied mass mortalities of *Crassostrea virginica* in Malpeque Bay, Canada and described the epizootiology and syndrome of the disease; Fraser (28) described the histopathology. A gradual buildup of resistance in offspring of surviving oysters produced a population which was free from the devastating effects of this disease (42). No pathogenic organisms were recognized in any of the mortalities mentioned above; all of the authors, however, suspected that infectious diseases were the cause of death in the 3 areas studied.

Prytherch (58) described a sporozoon, *Nematopsis ostrearum,* from *C. virginica* and believed that heavy infections caused mortality, but Sprague and Orr (68) and Feng (21) were unable to confirm his hypothesis. Takeuchi, Takemoto, and Matsubara (78) and Fujita, Matsubara, Hirokawa, and Araki (29, 30) associated bacterial infections with disease syndromes in *Crassostrea gigas* in Japan; and Tubiash, Chanley, and Leifson (85) fulfilled Koch's postulates with a bacteremia of larval oysters. Mackin (43) gave the 1st detailed description of the histopathology of an oyster disease caused by a fungus *Dermocystidium marinum.* The histochemistry and pigment cell development associated with *D. marinum* infection were reported by Stein and Mackin (75). Korringa (40) reviewed the history of oyster disease studies and discussed a disease of the shell of *O. edulis* caused by a fungus. Mackin, Korringa, and Hopkins (44) described the histopathology and mortality associated with infections by a flagellate *Hexamita* sp. in *O. edulis* in Holland, and Stein, Denison, and Mackin (76) reported on a transmission experiment with *Hexamita* sp. in *Ostrea lurida*. Comprehensive accounts of disease in oysters were reported by Mackin (46, 47). Hopkins (38), Sparks (64), Millar (49), Cheng and Burton (9), and Cheng (10, 11, 12) reported pathologic conditions associated with helminth infections in oysters. Studies of disease-associated haplosporidan parasites infecting oysters have been reported by Mackin (46), Haskin (33, 34), Haskin, Canzonier, and Myhre (35), Haskin, Stauber, and Mackin (36), Burton (8), Wood and Andrews (86), Andrews, Wood, and Hoese (2), Andrews (3, 4), Pereyra (57), Eble, (15), Myhre (51), Farley (18, 19, 20), Couch, Farley, and Rosenfield 13), Couch (14), and Barrow and Taylor (7).

Other investigations have dealt with the experimental aspects of disease processes in oysters. Takatsuki (77), Tanaka, Takasugi and Maoka (79), and Tripp, Bisignani, and Kenney (83) studied the nature and function of blood cells in oysters. Stauber (72), Tripp (80, 81, 82), and Feng (22, 23, 24, 25) discussed responses to injection of foreign material into *C. virginica* and the ultimate fate of the injected material. Feng (27) investigated the fate of a virus phage injected into oysters. Bang (5, 6) reported on phagocytosis and thrombosis in *C. virginica*. Stauber (73) and Tripp (84) studied immune response in oysters. Sparks and Pauley (67) reported on normal post-mortem changes produced experimentally, and Sparks, Pauley, Bates, and Sayce (65, 66) reported tumorous growths in *C. gigas*. Pauley and Sparks (55, 56) studied experimentally produced inflammatory response in *C. gigas*.

Problems in terminology. A review of the literature makes it apparent that ambiguity and misuse of terms have occurred in papers on oyster pathology due to the lack of definitive disciplinary terminology. The terms, "leucocyte," "leucocytosis," "eosinophilia," "leucocytopenia," and "inflammation" should be suppressed in descriptions of oyster pathology because they apply specifically and exclusively to vertebrate systems. Altho "leucocyte" has been used extensively in invertebrate pathology, it is by definition a type of vertebrate blood cell that lacks hemoglobin. "Hemocyte" is the appropriate term for an invertebrate blood cell (Webster's Unabridged Dictionary). "Leucocytosis," "eosinophilia," and "leucocytopenia" refer to the relative numbers of leucocytes or eosinophils in vertebrate blood samples and are based on established norms arrived at by standard methods. Methods have not been established for counting hemocytes in oysters from wild populations due to variability in heart rate and circulation caused by the semi-closed circulatory system, the poikilothermic nature of the animal, and other possible unknown factors (23, 24). "Hemocytosis" and "hemocytopenia" are suggested as terms denoting relative numbers of hemocytes in invertebrates when standard methods for counting hemocytes in oysters are established. The former term would apply to a supranormal number of hemocytes in the hemolymph or tissue and the latter term to a subnormal number. It appears to me that a ratio between phagocytes and hyaline hemocytes may prove to be the most meaningful indicator of systemic disease in oysters. Parenchymal cells in oysters have commonly been called Leydig cells (interstitial cells of the testis) but they were referred to as vesicular connective tissue cells by Galtsoff (31) and this term seems to me to be the better. Inflammation is a mammalian response characterized by redness, swelling, heat, cellular infiltration, and sometimes pain.

Figs 18-23. Histologic signs of disease. × 250. Fig. 18. Healthy oyster. A, connective tissue; B, hemolymph vessels; C, digestive diverticulum; D, ovary. Fig. 19. Healthy oyster. A, normal concentration of phagocytes; B, tubules of diverticula. Fig. 20. Initial infection of palp. A, infected epithelium; B, healthy epithelium. Note lack of cellular response in connective tissue. Fig. 21. Advanced infection. Note massive infiltration of connective tissue by hyaline hemocytes. Large dark staining cells are *M. nelsoni* plasmodia. Fig. 22. Massive necrosis and "metaplasia" of epithelia of diverticula in dying oyster. Fig. 23. Recovering oyster. Note massive concentration of pigment cells and absence of infiltration.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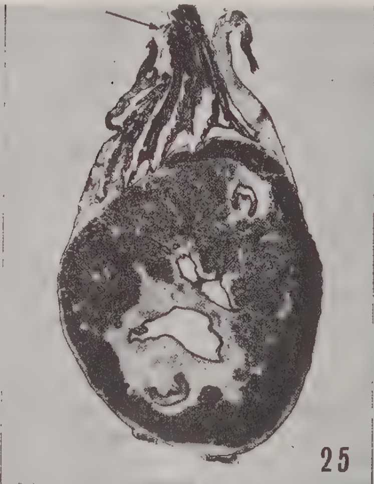
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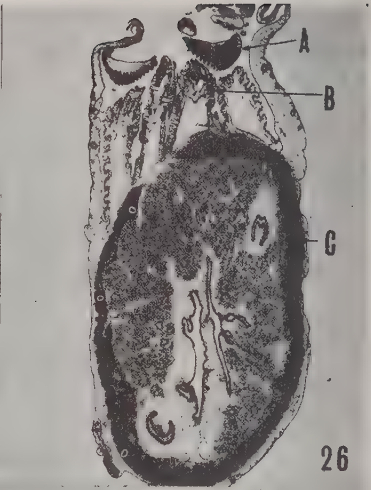

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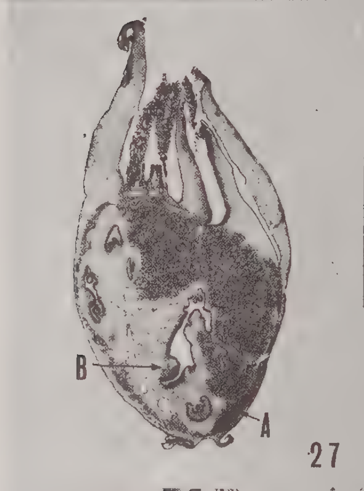

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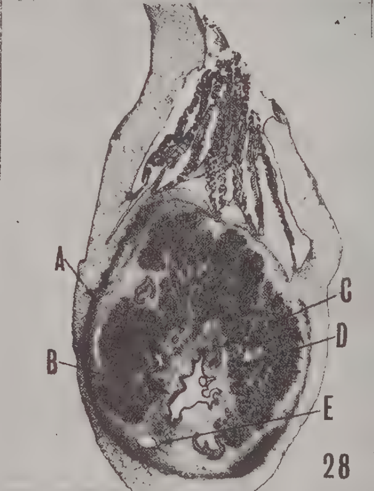

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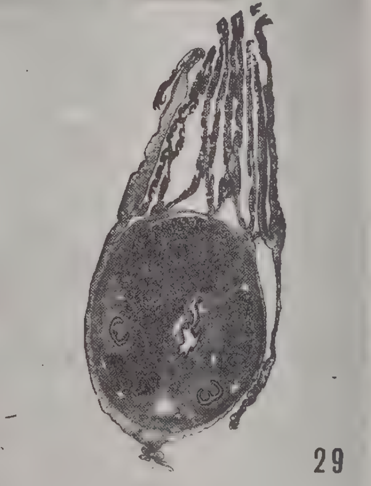
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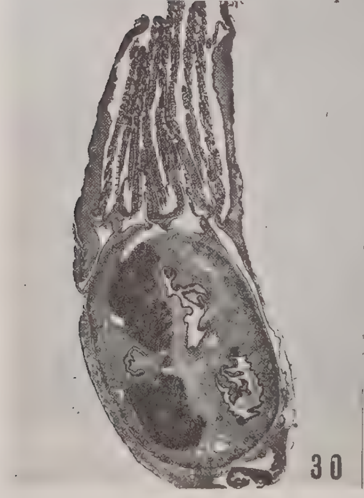
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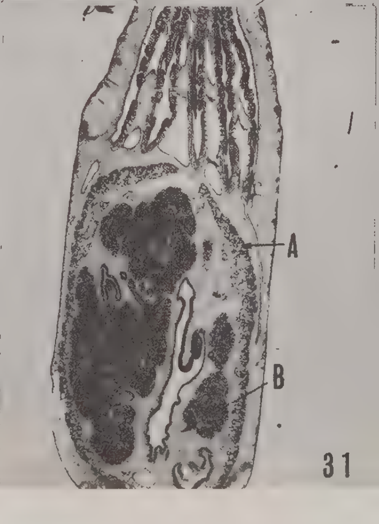

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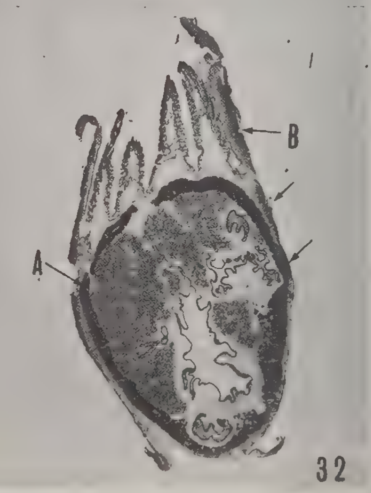

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The cellular infiltration (hyaline hemocyte reaction) associated with disease in oysters resembles inflammation histologically and probably can be considered an analogous but primitve response; however, since none of the other characteristics can be found, it is doubtful whether the term is appropriate. *Comparison of manifestations in different oyster diseases.* Table 2 summarizes the observations from previous investigations in oyster pathology. The signs and responses believed to be most significant have been listed. Quotation marks around citation numbers denote questionable interpretations.

Gross signs of disease (mantle recession, poor condition, pale digestive gland, pustules, epithelial exudates, conchiolin shell deposits, weak adductor muscle, and mortality) were studied intensively by early investigators but in recent years these characteristics have been largely neglected in favor of histologic and cytologic studies (Table 2). Gross signs most commonly associated with prolonged functional or infectious disease and mortality were: mantle recession, poor condition, pale digestive gland, and weak adductor muscle. Pustules have been seen in a number of diseases (28, 44, 52, 53, 60) but Orton (53) was the only investigator to relate "suppurations" (pustules) with "excretory deposits" (conchiolin shell desposits). A similar shell abnormality was described in *O. edulis* in Holland by Korringa (40) as a pathologic manifestation of a fungal infestation of the shell.

Weakness of oysters has been described as being associated with disease (16, 41, 52, 53, 60). It can be assumed that an oyster is dead, under natural conditions, when it cannot close its shell. Oysters in this condition are commonly called "gapers". Histologically, "gapers" usually show advanced signs of degenerative decay (necrosis, pyknosis, affinity for acid stains, and decrease in basic staining) and invasion of the tissue by saprophytic bacteria, ciliates and flagellates. Mortality from *M. nelsoni* disease is greatest in the summer, with a suggestion of seasonal peaks in June and August-September, and continues at low levels in late winter (4). Oysters in advanced stages of infection usually die at these times, but they may carry advanced infections for indefinite periods. Oysters with low-intensity, systemic infections also die during the mortality peaks, and especially in the late winter. This observation suggests that the pathologic manifestations involved in the cause of death are complex and not easily explainable by toxins or direct mechanical trauma.

The occurrence of pale digestive gland has been reported as a disease sign by others (Table 2). Hornell (39) and Engle (16) related the condition to stresses of low salinity; Orton (53), Roughley (60), Mackin (43) and Logie (41) described it as a sign of the various infectious diseases they studied. Shuster and Pringle (61) observed pale digestive glands, poor condition, and lack of growth in oysters subjected to prolonged cadmium exposure, and I have observed pale digestive gland as well as poor condition and mantle recession in starved oysters. Oysters collected during the late winter, when water temperatures normally remain below 5 C, also have pale digestive glands.

These observations seem to indicate that pale digestive glands are due to the absence of filtering, and consequent elimination by assimilation of food material in the digestive tract. Pale digestive glands caused by low salinity and exposure to cadmium may be a sign of prolonged valve closure in the face of adverse environmental conditions. Disease might produce the same effect thru pathologic or mechanical alteraton of the digestive system, reduced metabolic activity, or parasitic competition for nutrients. Mantle recession may result from prolonged starvation. The high intensity of *M. nelsoni* infection usually associated with advanced infections may lead to the use or breakdown of much of the stored glycogen of the host. It is also possible that pathologic modifications of the digestive system, causing inefficient assimilation and reduced metabolic activity, contribute to the apparent signs of starvation seen in advanced infections. The patterns of mortality and related pathology suggest that seasonal ecologic and physiologic (spawning) stresses on oysters in poor condition because of the disease are important factors of mortality.

Recognized mechanisms of defense in the oyster are primarily cellular responses by hemocytes and for the most part concern the hemolymph. Phagocytosis was the 1st response to be described (37) and has been studied extensively ever since (Table 2). Non-specific defenses involve phagocytosis or pinocytosis of foreign material, intracellular or extracellular digestion, migration of phagocytes to external epithelia and elimination by diapedesis (Table 2). An affected area is infiltrated by phagocytes when injury occurs and if a foreign object is too large to phagocytize, an abscess develops which is often encapsulated by fibroblasts. Further differentiation may produce an epithelium around the lesion. This process was described from the experimental studies of Pauley (54) and occurs naturally with cestode (12, 64) and watery cysts (47). Encapsulated material may be eliminated by digestion or ulceration. Occlusion, thrombosis and agglutination have been discussed by several authors (Table 2); possibly these terms were used to describe a synonymous response, for the mechanism causing this phenomenon may be a simple interlocking of phagocyte pseudopodia rather

Figs. 24-32. Histologic evidence for progressive stages of infection Photomacrographs of sections × 2.5. Fig. 24. Healthy oyster. Fig. 25. Initial infection; note congestion in gill lamellae (arrow). Fig. 26. Intermediate infection; note congestion in palp (A), gill lamella (B), and gonad (C). Darker area of gonad was not infected. Fig. 27. Intermediate infection; note congestion in gonad (A) and around stomach (B). Fig. 28. Intermediate infection; note congestion in gonad (A), around stomach (B), around gut (C), in digestive diverticula (D), and around blood sinus (E), Fig. 29. Advanced infection; note congestion in all tissues. Fig. 30. Terminal infection; note congestion in all tissues and fuzzy outlines of organ systems due to necrosis. Fig. 31. Remission of disease; note developing gonad and absence of congestion of tissues (A), and massive concentration of pigment cells (B). Fig. 32. Remission of infection; note developing gonad and absence of congestion elsewhere (A), and peripheral lesions adjacent to mantle (B). (This oyster was in the process of forming conchiolinous deposits on shell as shown in Fig. 3.)

TABLE 2. *Historical account of disease processes in oysters.*

Senior author	Mantle recession	Poor condition	Pale digestive gland	Pustules	Diapedesis	Conchiolin shell deposits	Weak adductor muscle	Mortality	Phagocytosis	Pinocytosis	Intracellular digestion	Cellular infiltration	Hyaline cell infiltration	Hemocytosis	Hemocytopenia	Occlusion	Thrombosis	Abscess	Fibrosis	Encystment	Ulceration	Agglutination	Immunity or resistance	Tissue lysis	Pigment cell formation	Hypertrophy	Edema	Mechanical disruption	Metaplasia	Pyknosis	Necrosis	Etiology
Herdman	—	—	—	—	37	—	—	—	37	—	—	—	—	37	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Copper pollution
Hornell	—	—	39	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Depressed salinity
Orton	—	53	53	53	53	53	53	53	53	—	—	53	—	"53"	—	—	53	53	53	53	—	—	—	—	—	—	—	—	—	—	53	Disease
Roughley	"60"	—	60	60	60	—	60	60	—	—	—	60	—	—	—	—	—	—	—	60	60	—	—	—	—	—	—	—	—	—	—	Disease
Takatsuki	—	—	—	—	77	—	—	—	77	—	77	—	—	—	—	—	77	—	—	—	—	—	—	—	77	—	—	—	—	—	—	Hemocyte study
Fraser	—	—	—	28	—	—	—	—	28	—	—	28	—	"28"	—	—	—	28	—	—	—	—	—	—	—	—	—	—	—	28	28	Disease
Prytherch	"58"	—	—	—	—	—	58	58	—	—	—	—	—	—	—	58	—	—	—	—	—	—	—	—	—	58	—	—	—	—	—	*Nematopsis ostrearum*
Engle	16	16	16	—	—	—	16	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Depressed salinity
Needler	52	52	—	52	—	—	52	52	—	—	—	—	—	—	—	—	—	52	—	—	—	—	52	—	—	—	—	—	—	—	—	Disease
Takeuchi	—	—	—	—	—	—	—	78	—	—	—	78	78	"78"	—	—	—	—	78	—	78	—	—	—	—	—	—	—	—	—	—	Bacterial disease
Stauber	—	—	74	—	72	—	—	—	72	—	73	—	—	"73"	—	72	72	—	—	—	—	—	73	—	—	—	—	—	—	—	—	Experimental studies
Mackin	47	47	43	44	45	—	—	43	43	—	—	42	—	"43"	—	44	—	44	43	45	43	—	—	43	45	—	—	43	—	44	43	Diseases
Korringa	"40"	—	—	—	—	40	—	40	—	—	—	"40"	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Disease and review
Fujita	—	—	—	—	—	—	—	—	30	30	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	30	Bacterial disease
Stein	—	—	—	—	—	—	—	75	76	—	—	—	—	"76"	—	76	—	—	—	—	—	—	—	76	75	—	76	—	—	—	76	Diseases
Menzel	48	48	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Diseases
Sprague	—	70	—	—	71	—	—	70	71	—	—	71	—	—	—	68	—	—	—	—	—	"71"	—	"71"	—	71	—	—	—	—	—	*Nematopsis* and *Minchinia*
Bang	—	—	—	—	—	—	—	—	5	—	—	"6"	—	—	—	—	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Experimental studies
Logie	41	—	41	—	—	—	41	41	—	—	—	—	—	—	—	—	—	41	—	—	—	—	41	—	—	—	—	—	—	—	—	Disease
Tripp	—	—	—	—	80	—	—	—	80	—	80	—	—	—	—	81	—	80	82	—	—	84	—	—	—	—	—	—	—	—	—	Experimental studies
Haskin	—	—	—	—	—	—	—	33	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	35	—	—	—	*M. nelsoni*
Feng	—	—	—	—	22	—	—	—	22	25	22	26	"26"	23	23	26	—	—	—	—	—	22	23	—	—	—	—	—	—	—	—	*Nematopsis* and experimental
Andrews	—	1	—	—	—	—	—	1	—	—	—	2	—	"2"	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	Diseases
Burton	—	—	—	—	—	—	—	—	—	—	—	—	—	"8"	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*M. nelsoni*
Wood	—	—	—	—	—	—	—	86	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*M. costalis*
Millar	—	—	—	—	—	—	—	49	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Trematoda
Myhre	—	—	—	—	—	—	—	—	—	—	—	50	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	50	—	—	—	*M. nelsoni*
Pereyra	—	—	—	—	—	—	—	57	—	—	—	57	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Haplosporidan
Sparks	—	63	—	—	—	—	—	—	67	—	—	67	—	—	—	—	—	—	64	64	—	—	—	67	—	67	67	67	67	67	67	Parasites and experimental
Galtsoff	31	31	—	—	31	—	—	31	31	—	—	—	—	—	—	31	—	—	—	—	—	—	—	—	31	—	—	—	—	—	—	Oyster studies
Haigler	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	32	—	—	—	—	—	—	Experimental studies
Pauley	—	—	—	54	—	—	—	54	54	—	54	54	—	54	—	54	54	54	54	54	54	—	—	54	54	54	54	54	—	54	54	Experimental studies
Eble	—	—	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*M. nelsoni*
Couch	13	13	13	—	—	—	—	13	—	—	—	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*M. nelsoni*
Cheng	—	—	—	—	—	—	—	—	—	—	—	9	—	11	—	—	—	—	12	12	—	—	—	—	10	—	—	9	—	—	—	Helminth diseases
Shuster	—	61	61	—	—	—	—	61	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2 ppm cadmium in tank
Farley	19	19	19	19	X	19	X	19	X	—	—	—	19	"X"	"X"	—	—	X	X	—	X	—	"X"	"X"	X	—	—	X	"X"	19	19	*M. nelsoni*

Disease manifestations, responses, and processes are listed across the top. Numbers represent literature citations of the respective authors in which the manifestations above them were discussed. Quotation marks denote unclear interpretation on my part or reservation on the point by the respective authors. X indicates an observation based on data from the present paper.

than a true thrombinogen (23). True hemagglutination of vertebrate red blood cells injected into oysters *in vivo* was described by Tripp (84).

The major responses in pathogenic invasions of the circulatory system appear to be massive numerical increases of hyaline hemocytes which infiltrate affected tissues (Table 2). Destructive processes which have been described from natural and experimental diseases are: lysis, hypertrophy, edema, mechanical disruption, metaplasia, pyknosis, and necrosis (Table 2). The functional significance and cause of pigment-cell formation associated with disease in the oyster continues to be a mystery (75). Resistance in oysters appears to be characterized by extracellular lysis of pathogens (23), lack of infiltration, aborted infections, phagocytosis, diapedesis, localized surface pustules, ulcers, and conchiolinous shell deposits.

Minchinia nelsoni disease has all of the gross characteristics of other oyster diseases described in the literature. Pigment-cell formation, phagocytosis, intracellular and extracellular digestion, surface abscesses (pustule formation), fibrosis, ulceration, diapedesis, and conchiolin shell deposits all appear to be associated with resistance. Mantle recession, pale digestive gland, poor condition, and infiltration by hyaline hemocytes are associated with active epizootic disease in susceptible oysters. Two types of hemocytes are generally recognized in oysters (31, 53, 73, 77, 79, 83): a large rapid-moving, amoeboid, granular, phagocytic form which I prefer to call a phagocyte and a small spherical, agranular, hyaline form with very limited mobility which I have referred to as a hyaline hemocyte. Takeuchi, Takamoto, and Matsubara (78) are the only previous investigators to associate the latter cell type with infiltration; however, I have been able to recognize this type of cell infiltrating affected tissue in many previously described and new diseases of *C. virginica, C. gigas* and *O. edulis*.

Hemocytopenia of phagocytes and hemocytosis of hyaline hemocytes appear to accompany advanced infections of *M. nelsoni*. Lysis, mechanical disruption, and possibly metaplasia of tissue are processes which occur with *M. nelsoni* infection but may be only indirectly responsible for death. Pyknosis and necrosis also are evident, but are actually signs rather than causes of death.

In 1959 the following institutions began a cooperative program of research on the causes of oyster mortality, especially *Minchinia nelsoni* (MSX): Agricultural and Mechanical College of Texas, College Station and Galveston, Texas; Hiram College, Hiram, Ohio; Natural Resources Institute of the University of Maryland, Solomons, Maryland; New Jersey Oyster Research Laboratory of Rutgers the State University, Bivalve and Cape May Court House, New Jersey; University of Delaware Marine Laboratory, Lewes, Delaware; the U. S. Bureau of Commercial Fisheries Biological Laboratory, Oxford, Maryland; and the Virginia Institute of Marine Science, Gloucester Point, Virginia. Annual workshop conferences with participants from the institutions named have helped to stimulate and shape my inquiry of the pathogenic signs of oyster diseases.

Dr. Melbourne R. Carriker advised and encouraged the establishment of the original disease-monitoring program, which ultimately provided much of the study material for this presentation; Drs. Aaron Rosenfield and Carl Sindermann advised and encouraged me throughout the study; Mrs. Virginia A. Liddell and Mrs. L. Cecelia Sullivan prepared all histological material; and the Maryland Department of Chesapeake Bay Affairs made available their boats and personnel for collection of oysters.

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(8) Fluctuations of Subarctic Circulation in Relation to Sockeye Salmon Fishery

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Although the actual physical basis and the time periods for effective coupling of motions of atmosphere and ocean are not precisely known, wind-stress transport in the Subarctic Region closely approximates, in direction and volume, transport obtained from oceanographic data when adequate stations are available. Monthly charts of total water transport induced by wind-stress over the North Pacific Ocean during the years 1950 to 1959 indicate fluctuations which cannot be obtained from fragmentary, non-synoptic oceanographic data. Average monthly transport for the 10-year period indicates that circulation in the Gulf of Alaska is weakest during spring, but flow in the Alaskan Stream and East Kamchatka Current is a minimum during summer. Frequent and appreciable deviations from average monthly transport occur throughout the region, but it is possible to predict fluctuations in circulation which are useful for fisheries problems.

The distribution and the migration routes of sockeye salmon, which are limited to the Subarctic Region, appear to be influenced by circulation patterns, particularly at the westward terminus of the Alaskan Stream. Recent evidence indicates that during both winter and summer, westward flow in the Alaskan Stream terminates at the Komandorskiy Ridge. Uncertainties in the extent of exchange of this boundary current with the Bering Sea and with water south of the Aleutian Islands, which is not predictable from local wind-stress, prevent a complete description of the circulation in this area.

A drifting telemetry buoy program, which will be operational in 1969, will provide synoptic oceanographic data and permit defining the relation between observed and theoretical flows throughout the Subarctic Region.

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A Radula Muscle Preparation from the Gastropod, *Kelletia kelletii*, for Biochemical Assays

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(1 Text figure)

THE MUSCLE BUNDLES, the odontophore muscle complex or radula muscle, which move the molluscan radula have been physiologically examined in isolated preparations from two species of carnivorous gastropods: *Busycon canaliculatum* (LINNAEUS, 1758) (HILL, 1956, 1958), a snail from the east coast of North America, and *Buccinum undatum* LINNAEUS, 1758 (FÄNGE & MATTISON, 1957, 1958), a snail common to European waters. These authors found that the muscle contracts under the influence of acetylcholine and is relaxed by 5-hydroxytryptamine and that rhythmic contractions of the muscle occur when acetylcholine and 5-hydroxytryptamine are added together. FÄNGE (1963) and FEDER & ARVIDSSON (1967) showed that aqueous extracts of the sea stars *Henricia sanguinolenta* (MÜLLER, 1776), *Marthasterias glacialis* (LINNAEUS, 1758) and *Asterias rubens* LINNAEUS, 1758 also induce strong contractions in the isolated radula muscle of *Buccinum undatum*. Because of the usefulness of this kind of radula muscle preparation for bioassay we sought one from a gastropod of the American west coast. This paper reports on the preparation and use of the radula muscle from the carnivorous snail *Kelletia kelletii* (FORBES, 1850) for biochemical assays.

Kelletia kelletii were collected by means of SCUBA at a depth of about 20 m on sandy ocean bottom, near the Scripps Institution of Oceanography, La Jolla, California. The bathymetric range of *K. kelletii* is known to extend from 18 to 62 m (ABBOTT, 1954). Some of the *Kelletia* were subsequently shipped to Hartnell College and used in experiments there. The radula muscle was prepared and mounted by a modification of the techniques of FÄNGE & MATTISON (1958), FÄNGE (1963), MATTISON & ARVIDSSON (1966), and FEDER & ARVIDSSON (1967) for isolating the radula muscle complex of *Buccinum undatum*. The final *Buccinum* muscle preparation included part of the proximal proboscis sheath which served for suspension of the muscle. *Kelletia* radula muscles prepared in this manner tended to behave erratically and showed a decreased sensitivity as compared to *Buccinum* radula muscles. This fact necessitated that the *Kelletia* radula muscle and the inner epithelial lining of the proboscis sheath be teased free of the sheath; the resulting preparation was more responsive and less erratic. The preparation was then suspended directly from the epithelial lining to the recording lever (Figure 1). The chamber was a plastic 30 cc syringe with the outlet enlarged to permit a rapid outflow when it was flushed. A lever with an arm 18 cm long and counterweighted with 2.0 g was used. The writing stylus was a fine glass rod of capillary size with a rounded tip. The muscle was mounted to the lever at its proximal end by a cotton thread through the epithelial tissue and to the glass rod at its oral end by a small loop from the radula sheath tissue. During perfusion sea water was either removed by aspiration or allowed to overflow the chamber. All other details of the experimental setup were the same as those described for radula muscle preparations of *Buccinum undatum* by FEDER & ARVIDSSON (1967).

Specimens of the sea star *Pisaster ochraceus* (BRANDT, 1835) were taken either from pilings off the pier at Scripps Institution of Oceanography, or from rocky reefs off La

Jolla, and from intertidal areas in Monterey Bay, California. The sea star *Pycnopodia helianthoides* (Brandt, 1835) was collected in intertidal areas in Monterey Bay. Extracts were obtained by the same procedures used by Feder & Arvidsson (1967) for the preparation of *Marthasterias glacialis* test solutions. Living sea stars were washed in tap water, frozen, and then thawed; the resultant cloudy exudate was collected and centrifuged. The clear supernatant fluid was used in all tests.

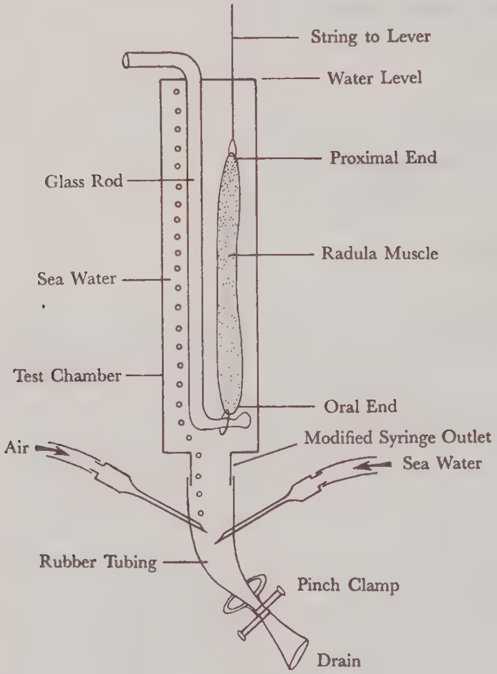

Figure 1

Diagram of the mounted radula muscle preparation

The *Kelletia* radula muscle contracted in the presence of acetylcholine of which the final concentration was 5×10^{-8} g/ml. Extracts of *Pisaster ochraceus* also caused the radula muscle of *Kelletia* to contract; the strength of the contractions varied roughly with amount of extract added. After addition of acetylcholine or *P. ochraceus* extract the contraction could be reversed immediately by 3×10^{-7} g/ml (final concentration) of 5-hydroxytryptamine. Strong, rhythmical contractions followed the initial relaxation. Similar responses of *Kelletia* muscle to *Pycnopodia* extracts were found in preliminary experiments. Responses, however, were always of greater magnitude to *Pycnopodia* than to *Pisaster ochraceus,* whether as contractions in response to the extracts or rhythmic contractions in response to the extracts after addition of 5-hydroxytryptamine. The amplitude of muscle contraction after additon of *Pycnopodia* extract was 2 to 3 times greater than that caused by addition of identical volumes of *Pisaster ochraceus* extract.

Sensitivity of muscles varied with time; in general, older preparations, 24–48 hours old maintained in a water bath at 10° C, were more sensitive. In addition, muscle preparations responded only when a certain "threshold" concentration (40 microliters in a final volume of 30 ml of sea water) of *Pisaster* extract was reached. An addition of sea star extract 5 times the threshold amount (i. e. 200 microliters in a final volume of 30 ml of sea water) frequently caused an extremely strong contracture from which the muscle often did not recover when the sea water in the bath chamber was renewed. Thus, like *Buccinum* muscle preparations, responses were quantitative only within a narrow range of extract additions.

The successful isolation of the radula muscle complex of *Kelletia kelletii* and its subsequent use in assay increases the number of available preparations of this type to three; *Busycon canaliculatum* and *Buccinum undatum* represent the other two species. The *Kelletia* preparation is very similar to that of *Buccinum,* and the responses of the radula muscles of the two species also are similar. It is probable that other carnivorous snails have radula muscles suitable for physiological and pharmacological studies.

ACKNOWLEDGMENTS

This work was supported by a National Science Foundation Research Participation Grant to one of us (H. M. F.), and was accomplished at the Bureau of Commercial Fisheries, Fishery-Oceanography Center, La Jolla, California. We thank Mr. Daniel Tam of Hartnell College and Mr. William Vlymen of the Scripps Institution of Oceanography for their very able technical assistance, and Mr. George Crozier of the Scripps Institution of Oceanography and Mr. Robert Bowers of the Scripps Tuna Oceanography Research Program for collection of experimental animals.

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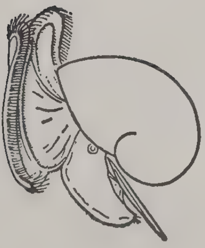

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U. S., Japan To Hunt Salmon Routes

By Robert French
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U.S. RESEARCH VESSEL **George B. Kelez will be used by scientists in joint study of Pacific salmon this spring. Japanese will conduct similar work from two of their vessels.**

SEATTLE, WASH. — Fishery biologists from Japan and the United States will join forces for a fishery research cruise in the North Pacific Ocean this spring.

The knowledge gained during the cruise should aid the scientists in making better estimates of the number of Bristol Bay sockeye salmon available for harvest by fishermen in a given year.

During the three-month, three-vessel cruise, the researchers will study the salmon in their ocean environment and chart their migration routes and distribution in the ocean. The U. S. biologists, employees of the Bureau of Commercial Fisheries Biological Laboratory here, will be aboard the laboratory's 550-ton research vessel George B. Kelez.

Biologists from the Japan Fisheries Agency will work from two smaller vessels, the 150-ton Wakashio-Maru and the 220-ton Hokko-Maru.

The Kelez left Seattle on April 2 and was to be joined by the Japanese vessels on the fishing grounds later in the month. The Japanese vessels will remain until early June; the Kelez will return to her home port early in July.

The men on the joint cruise hope to find out which currents and water masses the salmon inhabit south of the Aleutian Islands. They will test the theory that salmon follow specific currents while feeding in the ocean and while migrating to their spawning grounds.

U.S., CANADA, JAPAN

In 1953, the United States and Japan, together with Canada, formed the International North Pacific Fisheries Commission (INPFC) to further the development and conservation of the fisheries of the North Pacific Ocean. Under INPFC provisions, Japan agreed not to fish for salmon east of the abstention line at 175° west longitude. Fishery researchers have since learned that sockeye salmon spawned in Bristol Bay streams migrate to the west of the abstention line. The joint cruise should help determine what part of the Bristol Bay run thus becomes available for harvest by Japanese fishermen.

Japan will record data on the distribution of salmon in the western part of the research area. The United States will record fisheries data from the eastern part and oceanographic information for all areas under study.

The oceanographers will study the size and location of the currents and determine their boundaries.

Salinity and temperature at various depths will be recorded on all cruise tracks. Biological samplings will be made. The minute organisms on which fish feed will also be collected and studied.

The Kelez will fish a basic string of 32 shackles (1.8 miles) of gillnetting with five mesh sizes from 5¼ to 2½", stretch measure. The Japanese vessels will fish a basic string of either 50 tans (1.6 miles) or 100 tans (3.2 miles), consisting of similar mesh sizes.

Catches will be classfied by species for each mesh size. Lengths and scale samples will be taken to determine the age of each fish. U. S. scientists will also collect blood samples which provide clues to the river of origin of the salmon, and pituitary glands to determine which fish will return to spawn and which fish will remain in the ocean for another year.

Skipjack Tuna Subpopulation Identified by Genetic Characteristics in the Western Pacific

by

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As a part of the Pacific-wide studies of the population structure of the skipjack tuna (Katsuwonus pelamis), more than 2,500 blood specimens have been collected from areas off the northeastern coast of Japan, Okinawa, and the Mariana and Palau Islands in the western Pacific Ocean. Genetic compositions of the blood group and serum group systems for the specimens were compared between different areas. The results indicated that 1) no significant heterogeneity was seen in all the genetic systems used within the western Pacific, and 2) gene frequencies of the serum esterase system of the samples from the western Pacific are significantly different from those of the central Pacific (Hawaii and Line Islands) and the eastern Pacific (Baja California). On the basis of these observations as well as other available biological information, the skipjack tuna population structure in the western Pacific is discussed.

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Serum Esterase Groups of Pacific and Atlantic Tunas

KAZUO FUJINO AND TAGAY KANG

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Starch-gel electrophoretic analysis of serum specimens of 8201 skipjack tuna (*Katsuwonus pelamis*), 187 albacore (*Thunnus alalunga*), 107 bigeye tuna (*T. obesus*), and 65 yellowfin tuna (*T. albacares*) taken from the Pacific and Atlantic oceans demonstrated individual genetic variations in the serum esterase component within each species. The esterase system proved to be independent of any known blood group systems, of sex, and of size of fish in each species.

In skipjack tuna extensive data allowed an application of the system to the problem of identifying subpopulations, or isolated breeding populations. Heterogeneity tests for the gene frequencies of the esterase system showed: a) a population in the equatorial Atlantic is different from any populations recognized in the Pacific; b) eastern Pacific (Baja California) specimens were indistinguishable from those of Hawaiian waters; and c) the western Pacific (Japan and Palau) has at least one subpopulation different from the population in Hawaiian waters.

INTRODUCTION

THE technique of starch-gel electrophoresis, developed by Smithies (1955) for analysis of serum protein, detects individual genetic differences among various humoral and cellular proteins of animals (Whipple, 1964). Advanced histochemical staining techniques have accelerated the application of electrophoresis to biochemical genetics of general proteins and enzymes in humans and various other species of animals. Markert and Hunter (1959) published the first studies of esterase, in mouse tissue.

Several electrophoretic studies of fishes have been conducted. Nyman (1965) described polymorphisms of serum esterase of bleak, roach, and cod. Møller and Naevdal (1966) published on polymorphisms of transferrin and Sick (1965) and Frydenberg *et al.* (1965), on hemoglobin of Atlantic gadoid fishes. Keyvanfar (1962) observed variations in electrophoretograms of serum proteins in albacore and bluefin tuna from the Atlantic Ocean and the Mediterranean Sea.

The present paper reports on the finding of genetic variations in serum esterase components of skipjack tuna (*Katsuwonus pelamis*), albacore (*Thunnus alalunga*), bigeye tuna (*T. obesus*), and yellowfin tuna (*T. albacares*), as demonstrated by starch-gel electrophoresis, and on some applications of these findings to the identification of isolated breeding populations, or subpopulations, of tunas. Concurrent studies were made on blood groups of tunas and will be reported elsewhere (Fujino and Kazama, MS).

MATERIALS AND METHODS

Tuna serum.—Skipjack tuna serum or supernatant specimens used in the present study include two lots of 117 specimens taken from the equatorial Atlantic (12°–19° N, 61°–67° W) in February through April, and November 1966; six lots of 386 off Baja California in August through September 1965; 79 lots of 7004 from Hawaiian waters between April 1965 and October 1966; five lots of 398 from Japanese waters in September through November 1966; and four lots of 296 from the sampling station on the Palau Islands in November and December 1966. These specimens were collected from fish caught by the Laboratory's research vessel CHARLES H. GILBERT (CHG) and commercial fishing boats.

Albacore include 84 specimens taken by the Japanese research vessel SHOYO MARU from the Atlantic Ocean (14° N–30° S, 29°–31° W) in December 1965 and January 1966 and 103 specimens taken by commercial fishing boats from the eastern Pacific in July and August 1965. A total of 107 bigeye tuna and 65 yellowfin tuna specimens was taken from Hawaiian waters by CHARLES H. GILBERT and commercial fishing boats in July and March 1966, respectively.

Serum specimens were taken and preserved according to Fujino (1966). When large numbers of specimens were to be processed,

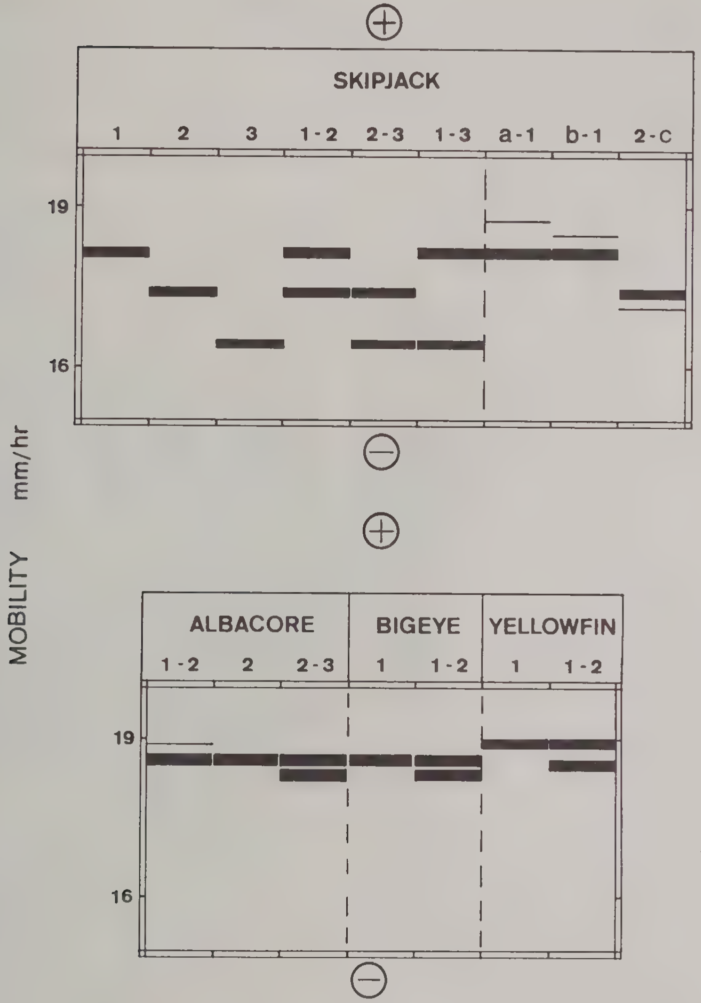

Fig. 1. Relative mobility of serum esterase bands in skipjack tuna (*Katsuwonus pelamis*), albacore (*Thunnus alalunga*), bigeye tuna (*T. obesus*), and yellowfin tuna (*T. albacares*).

we used the supernatant of the whole blood specimen, which had been taken primarily for blood group study and refrigerated or frozen in anticoagulant solution (Fujino and Kazama, MS). The supernatant was dialyzed against 1.5% saline and then concentrated by dehydrating with carbowax (Fujino and Cushing, 1959) up to approximately the original serum concentration.

Electrophoresis.—Horizontal starch-gel electrophoresis was performed at room temperature. The buffer solution described by Ashton (1965) was modified. The concentration of lithium hydroxide was doubled for the electrolyte, giving a pH of 8.2. For the gel buffer, the proportion between the above solution and the solution of citric acid and tris aminomethane was changed from 1:9 to 1:3. Twelve percent starch-gel (Starch-Hydrolysed, Connaught Medical Laboratories, Toronto) was prepared by following Kristjansson (1963). Upon cooling the gel was sliced horizontally to give a uniform three-mm thickness.

Increasing voltages of electric current, from 14 to 18 v/cm of gel, were applied by maintaining a current intensity of no more

Table 1. Incidence of Six Phenotypes of Skipjack Tuna Serum Esterase (E_{SJ}) in Representative Hawaiian Samples.

Lot No.	Phenotypes												Total	Alleles[2]		
	1		1–2		2		2–3		3		1–3					
	O[1]	E[1]	O	E	O	E	O	E	O	E	O	E		E^1_{SJ}	E^2_{SJ}	E^3_{SJ}
CHG-81																
2	23	22.2	44	45.5	24	23.3	1	1.0	0	0.0	1	1.0	93	0.489	0.500	0.011
12	21	21.4	47	47.4	27	26.2	0	1.1	0	0.0	2	0.9	97	0.470	0.520	0.010
13	35	34.6	82	81.5	47	47.9	3	1.7	0	0.0	0	1.3	167	0.455	0.536	0.009
15	23	22.1	47	48.8	28	27.1	0	0.0	0	0.0	0	0.0	98	0.475	0.525	0.000
CHG-91																
5	26	25.3	45	46.4	22	21.5	1	0.8	0	0.0	1	1.0	95	0.516	0.474	0.010
8B	26	23.3	39	45.0	25	21.8	1	1.4	0	0.0	2	1.5	93	0.500	0.484	0.016
10	4	5.8	20	16.5	10	11.7	0	0.0	0	0.0	0	0.0	34	0.412	0.588	0.000
12	9	11.8	36	30.2	17	19.2	0	1.6	1	0.0	1	1.2	64	0.430	0.548	0.022
14	9	7.7	24	25.8	22	21.6	2	1.2	0	0.0	0	0.7	57	0.368	0.615	0.017
17	9	9.1	29	28.2	21	21.8	2	1.2	0	0.0	0	0.7	61	0.386	0.598	0.016

[1] O = observed; E = expected. [2] $E^1_{SJ} + E^2_{SJ} + E^3_{SJ} = 1$.

than 2.6 ma/cm width of the gel for approximately three hr. The system was kept cool during the run by placing a tray of ice in a compartment of the plastic gel holder.

Staining.—The formula for the staining solution described by Markert and Hunter (1959) was modified. The solution consisted of: 200 ml 0.075 M monobasic and 0.025 M dibasic sodium phosphate solution; four ml acetone-water (1:1) containing 1% alpha-naphthyl acetate; and 50 mg diazonium salt, Fast Blue RR. The gel was soaked in the solution for 5–10 min at room temperature. The stained gel was fixed by soaking in a solution of methanol-water-acetic acid (5:5:1 in volume) for 30 min.

Electrophoretic Patterns of Esterase Bands

Six esterase bands were recognized in skipjack tuna, three in albacore, and two each in bigeye and yellowfish tunas. Relative mobility of these bands is shown in Fig. 1. Details are described by species.

Skipjack tuna.—Three clear bands, named 1, 2, and 3 in the order of their decreasing mobility, occurred regularly. Six individual differences, that is, 1, 1–2, 2, 2–3, 3, and 1–3, were observed. We proposed the hypothesis that these six phenotypes are determined by three codominant alleles. To test the hypothesis, the Hardy-Weinberg law was applied to all specimens taken from Hawaiian waters. Failure to find statistically significant differences between observed and expected incidences of phenotypes supports the hypothesis that the six phenotypes form a system (E_{SJ} system) determined by three alleles, E^1_{SJ}, E^2_{SJ}, and E^3_{SJ}. Examples of the frequency distribution of these alleles are shown in Table 1.

In addition to three clear bands, three faint bands—that is, bands a and b (faster than band 1) and c (slower than band 2) —occurred only in combination with the regular bands (Fig. 1). Table 2 summarizes the incidences of the subgroups, consisting of the three regular and the two rare bands a and b, for the Hawaiian samples accumulated from April 1965 to October 1966. (Only two instances of the third rare band c occurred, in combination with band 2; they are not listed in Table 2.) To obtain expectations, an additional two alleles which determine the rare bands a and b were proposed. Good consistency between the observed and expected incidences in this table suggests that the rare bands a and b belong to the E_{SJ} system. Tables 3 and 4 show that the E_{SJ} system is independent of sex and size groups. There is no apparent correlation between the esterase system and the known blood group systems B and Y (Sprague and Holloway, 1962; Fujino and Kazama, MS).

TABLE 2. HARDY-WEINBERG ANALYSIS OF E_{SJ} SYSTEM IN SKIPJACK TUNA (TOTAL HAWAIIAN SAMPLES). * Theoretically possible, but never observed.

Phenotypes	Subgroups	Incidence	
		Observed	Expected
*	a	0	0.03
	a–b	0	0.03
	b	0	0.01
1	a–1	11	12.86
	b–1	8	8.12
	1	1621	1635.99
1–2	1–2	3409	3381.65
2	a–2	16	13.29
	b–2	9	8.39
	2	1736	1747.50
2–3	2–3	90	98.66
3	a–3*	0	0.38
	b–3*	0	0.24
	3	4	1.39
1–3	1–3	100	95.46
Total		7004	7004.00

TABLE 3. RELATION OF E_{SJ} SYSTEM TO SEX IN SKIPJACK TUNA. ($\chi^2 = 3.385$.)

Phenotypes	Male		Female	
	Observed	Expected	Observed	Expected
1	95	96.4	89	87.6
1–2	208	214.9	202	195.1
2	136	127.3	107	115.7
2–3	4	5.2	6	4.8
3	1	0.5	0	0.5
1–3	4	3.7	3	3.3
Total	448	448.0	407	407.0

Gene frequencies for the regular bands of all 96 lots of specimens were subjected to intra-areal and inter-areal heterogeneity tests (chi-square test for contingency table) —Table 5. Owing to the large numbers of fish involved, individual lots taken from Hawaiian waters are not shown in this table. Table 6 summarizes the results of the heterogeneity tests for frequencies of genes E^1_{SJ}, E^2_{SJ}, and E^3_{SJ}. Because of low incidences, E^3_{SJ} was combined with E^2_{SJ}.

The intra-areal tests showed that no significant heterogeneity was observed in any of the five areas. The inter-areal tests for the neighboring areas showed that heterogenity was significant in the combinations of samples of eastern Pacific–Atlantic, Hawaii–Japan, and Hawaii–Palau, but not significant in the combinations of eastern Pacific–Hawaii and Japan–Palau.

Fig. 2 summarizes ranges, means, and standard deviations of frequencies of the alleles E^1_{SJ} for samples from different areas. The above statistical tests and Fig. 2 demonstrate that 1) the Atlantic specimens are distinguishable from those of the eastern Pacific; 2) the eastern Pacific specimens fall within the range of the Hawaiian; 3) the Japanese are distinguishable from the Hawaiian; and 4) the Palauan are also distinguishable from the Hawaiian, but have a distribution that partially overlaps that of the Japanese.

For the two examples, Japan–Palau and eastern Pacific–Hawaii, in which the heterogeneity was not significant in the above tests, a statistical comparison (*t*-test) was made of the mean values of gene frequency. The differences of mean frequencies of the allele E^1_{SJ} were significant for the Japan–Palau example ($t = 2.722$, 7df $0.01 > P$) but did not reach the significant level of 5% for the eastern Pacifi–Hawaii example despite the low figure of the probability ($t = 1.936$, 83df $0.10 > P > 0.05$). This result suggested the necessity of acquiring extensive additional population data on genetic systems, particularly in the western and eastern Pacific, before describing conclusively the relation of entire population structures.

Albacore.—Two bands, named 2 and 3, occurred commonly in the Atlantic and the eastern Pacific samples. The fastest band—1—occurred in the Atlantic samples only. The combinations of these bands expressed three phenotypes, 1–2, 2, and 2–3 in the Atlantic, and two, of 2 and 2–3, in the eastern Pacific samples. Hardy-Weinberg analyses of these samples, shown in Table 7, suggest that the three recognized bands are determined by three codominant alleles. Under this hypothesis it is theoretically possible for six phenotypes to occur in this system (E_{AL} system). In Table 7 are also shown frequencies of three genes E^1_{AL}, E^2_{AL}, and E^3_{AL} of the E_{AL} system. Table 8 shows that the E_{AL} system is independent of sex. There is no apparent correlation between the esterase system and the Tg blood group system.

In contrast to a significantly different incidence of the Tgl factor of the Tg blood

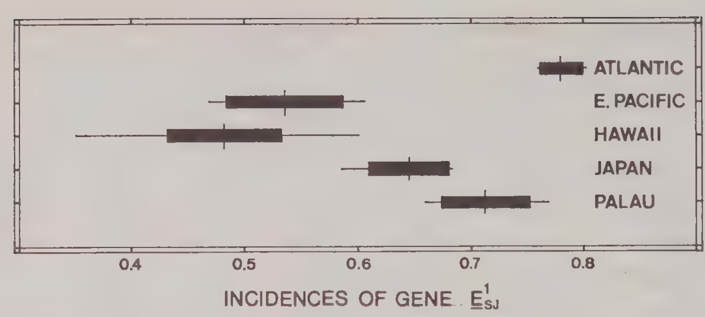

Fig. 2. Skipjack tuna (*Katsuwonus pelamis*) serum esterase gene (E^1_{SJ}) frequencies in different areas.

groups between the Atlantic and the Pacific albacore (Suzuki, 1962) differences of gene frequencies of the E_{AL} system between the two areas are not significant, except for the low incidence of occurrence of the gene E^1_{AL} of the fastest band in the Atlantic sample (Table 7).

Bigeye tuna.—Two bands, named 1 and 2, occurred. Two phenotypes of 1 and 1–2 were observed in the Hawaiian sample. Results of Hardy-Weinberg analysis suggested that the two bands were determined by two codominant allelic genes of the E_{BE} system (Table 9). Insufficient data were available for analysis of relation of the E_{BE} system to sex and size groups.

Yellowfin tuna.—Two individual differences were observed as a combination of two bands, fast and slow. Hardy-Weinberg analysis showed that these bands were controlled by two codominant genes of a genetic system (E_{YF} system)—Table 10. No data were available on the relation of the E_{YF} system to sex and size groups.

TABLE 4. RELATION OF E_{SJ} SYSTEM TO SIZE GROUPS IN SKIPJACK TUNA. ($\chi^2 = 7.311$.)

Phenotypes	Fork Length (cm)									
	<40		41–50		51–60		61–70		>71	
	O[1]	E[1]	O	E	O	E	O	E	O	E
1	6	8.1	64	63.4	10	9.0	14	14.8	8	6.7
1–2	21	17.4	135	137.0	17	19.4	34	31.9	13	14.5
2	9	10.0	77	78.4	13	11.0	18	18.3	9	8.3
2–3	0	0.3	4	2.5	0	0.4	0	0.6	0	0.3
3	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
1–3	0	0.2	3	1.7	0	0.2	0	0.4	0	0.2
Total	36	36.0	283	283.0	40	40.0	66	66.0	30	30.0

[1] O = observed; E = expected.

TECHNICAL NOTE

At the beginning of our investigation, we ran duplicate tests on two types of samples from each of several hundred fishes. These samples consisted of serum centrifuged from the fresh blood and of supernatant obtained by dialyzing the frozen blood. Results from the two types of specimens were always identical.

By thus establishing that the supernatant specimens give results as valid as serum, we have become convinced that a single collection of whole blood from an individual fish permits analyses of both blood groups and serum esterase. The consequent extension of our ability to study two independent genetic systems should improve population identification without additional effort in collecting and preserving materials.

IDENTIFICATION OF SKIPJACK TUNA SUBPOPULATIONS OF DIFFERENT GEOGRAPHICAL AREAS

The differential incidences of esterase-determinant alleles, in conjunction with other information, allow the following interpretations with regard to identification of subpopulations: 1) The incidences of the esterase alleles of the equatorial Atlantic specimens were significantly different from any specimens obtained from the Pacific. This suggested that the equatorial Atlantic population is different from any populations recognized in the Pacific. 2) The gene frequencies of the esterase system of the eastern Pacific specimens fall within the range of the Hawaiian specimens. Long-distance movements of three tagged skipjack tuna indicated that these fish migrate from the eastern Pacific to the central Pacific (Schaefer, 1963; Inter-American Tropical Tuna Commission, 1964). These supplemental pieces of evidence

TABLE 5. INCIDENCE OF E_{SJ} SYSTEM IN SKIPJACK TUNA FROM VARIOUS AREAS OTHER THAN HAWAII.

Area and Lot No.	Phenotypes 1	1–2	2	2–3	3	1–3	Total	Alleles[1] E^1_{SJ}	E^2_{SJ}	E^3_{SJ}
Atlantic										
1	54	31	6	0	0	1	92	0.761	0.234	0.005
2	15	10	0	0	0	0	25	0.800	0.200	0.000
Eastern Pacific										
1	16	38	16	0	0	1	71	0.500	0.493	0.007
2	45	93	50	1	0	4	193	0.484	0.502	0.014
3	16	28	8	1	0	0	53	0.566	0.424	0.010
4	7	9	3	0	0	0	19	0.605	0.395	0.000
5	5	9	2	0	0	1	17	0.589	0.382	0.029
6	7	16	9	0	0	1	33	0.470	0.516	0.014
Japan										
1	42	36	15	0	0	2	95	0.642	0.347	0.011
2	34	43	18	0	0	0	95	0.584	0.416	0.000
3	26	20	7	0	0	0	53	0.679	0.321	0.000
4	38	33	9	0	0	2	82	0.677	0.311	0.012
5	35	27	11	0	0	0	73	0.664	0.336	0.000
Palau										
1	37	33	11	0	0	0	81	0.660	0.340	0.000
2	33	24	6	1	0	1	65	0.700	0.285	0.015
3	44	26	4	0	0	0	74	0.770	0.230	0.000
4	40	29	6	1	0	0	76	0.717	0.276	0.007

[1] $E^1_{SJ} + E^2_{SJ} + E^3_{SJ} = 1$.

strengthen the hypothesis that a skipjack tuna resource is common to the eastern Pacific and the central Pacific (Rothschild, 1965). A statistical comparison (*t*-test) of the samples from Hawaii and Baja California showed low probability ($0.10 > P > 0.05$), although the difference of mean frequencies of the allele E^1_{SJ} did not reach the significant level of 5%. This result suggested that we need more extensive population data on

TABLE 6. RESULTS OF HETEROGENEITY TESTS SUMMARIZED FOR GENE FREQUENCIES OF E_{SJ} SYSTEM IN SKIPJACK TUNA.

Area	χ^2	df	Probability
Intra-areal			
Atlantic	0.183	1	$0.70 > P > 0.50$
E. Pacific	2.689	5	$0.80 > P > 0.70$
Hawaii	62.155	78	$0.90 > P > 0.80$
Japan	2.246	4	$0.70 > P > 0.50$
Palau	2.336	3	$0.70 > P > 0.50$
Inter-areal			
E. Pacific-Atlantic	27.760	7	$0.001 > P$
E. Pacific-Hawaii	68.904	84	$0.90 > P > 0.80$
Hawaii-Japan	116.061	83	$0.05 > P$
Hawaii-Palau	126.711	82	$0.005 > P$
Japan-Palau	5.971	8	$0.70 > P > 0.50$

TABLE 7. HARDY-WEINBERG ANALYSIS OF ALBACORE SERUM ESTERASE (E_{AL}).

Phenotypes		Atlantic Observed	Expected	Eastern Pacific Observed	Expected
1		0	0.0	0	0.0
1–2		2	1.9	0	0.0
2		76	76.1	95	95.1
2–3		6	5.8	8	7.7
3		0	0.1	0	0.2
1–3		0	0.1	0	0.0
Total		84	84.0	103	103.0
Alleles[1]	E^1_{AL}		0.012		0.000
	E^2_{AL}		0.952		0.961
	E^3_{AL}		0.036		0.039
χ^2			0.212		0.205

[1] $E^1_{AL} + E^2_{AL} + E^3_{AL} = 1$.

TABLE 8. RELATION OF E_{AL} SYSTEM TO SEX OF ALBACORE (ATLANTIC SAMPLES). ($\chi^2 = 0.090$.)

Phenotypes	Male		Female	
	Observed	Expected	Observed	Expected
1–2	1	1.1	1	0.9
2	39	38.6	32	32.4
2–3	3	3.3	3	2.7
Total	43	43.0	36	36.0

TABLE 10. HARDY-WEINBERG ANALYSIS OF YELLOWFIN TUNA SERUM ESTERASE (E_{YF}). ($\chi^2 = 0.006$.)

Phenotypes	Observed	Expected
1	63	63.1
1–2	2	1.9
2	0	0.0
Total	65	65.0

genetic systems, particularly from the eastern Pacific, before we can accurately describe the relation of skipjack tuna resources of the eastern Pacific and the central Pacific—say, *e.g.*, whether the entire portion or segments of populations are common to both areas. 3) Samples from the western Pacific (Japan and Palau) were distinguishable from Hawaiian samples by gene frequencies of serum esterase. This result suggested that the western Pacific has at least one subpopulation that is different from the population in Hawaiian waters. Further population data should be accumulated to learn the relation between fish from Palau and Japan.

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TABLE 9. HARDY-WEINBERG ANALYSIS OF BIGEYE TUNA SERUM ESTERASE (E_{BE}). ($\chi^2 = 0.465$.)

Phenotypes	Observed	Expected
1	93	93.5
1–2	14	13.1
2	0	0.4
Total	107	107.0

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TRANSFERRIN GROUPS OF TUNAS

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TRANSFERRIN polymorphism has been demonstrated by gel electrophoresis in many vertebrates. These include men (SMITHIES and HILLER 1959), monkeys (GOODMAN and POULIK 1961), cattle (ASHTON 1958; SMITHIES and HICKMAN 1958), sheep and goats (ASHTON and FERGUSON 1963; EFREMOV and BRAEND 1964), horses (BRAEND and STORMONT 1964), burros (NIECE and KRACHT 1967), pigs (ASHTON 1960a), mice (ASHTON and BRADEN 1961), antelopes (ASHTON and CARR 1965), harp seals (NAEVDAL 1965), doves (MUELLER 1961), chickens (OGDEN, MORTON, GILMOUR and MCDERMID 1962), and gadoid fishes (MØLLER and NAEVDAL 1966; MØLLER 1966). BARRETT and TSUYUKI (1967) have found polymorphisms of transferrin in several scombroid fishes—yellowfin tuna, skipjack tuna, albacore, and bonito.

The animals most thoroughly studied have been domestic cattle. Transferrin phenotypes have been shown to be associated with differences in fertility and fetal mortality (ASHTON 1959), and maternal-fetal incompatibility (ASHTON 1965). Transferrin phenotypes have also been associated with differences in the production of milk and butterfat (ASHTON 1960b; ASHTON, FALLON and SUTHERLAND 1964).

This paper (1) describes transferrin polymorphisms in skipjack tuna (*Katsuwonus pelamis*), southern bluefin tuna (*Thunnus maccoyi*), and yellowfin tuna (*T. albacares*) from the Atlantic and Pacific Oceans; (2) presents evidence of differential adaptive values of phenotypes in skipjack tuna; and (3) discusses possible mechanisms of maintaining transferrin polymorphism in a randomly mating population.

MATERIALS AND METHODS

Tuna serum: Skipjack serum or supernatant (plasma obtained by dialysing whole blood specimen frozen in glycerol solution, FUJINO 1966) specimens include: 3 lots of 213 specimens taken from the tropical Atlantic Ocean (latitude 12° N–19° N, longitude 61° W–68° W) from February through November 1966; 27 lots of 2,257 specimens from Hawaiian waters taken between April 1965 and August 1967; 5 lots of 401 specimens from Japanese waters taken from September through November 1966; and 20 lots of 1,495 specimens taken from Palau from November 1966 through November 1967. These samples were collected from fish caught by the Laboratory's research vessel *Charles H. Gilbert* and commercial fishing boats.

Southern bluefin samples were 302 collected from waters off Australia in 1963 and 1964 by the staff of the Commonwealth Scientific and Industrial Research Organization, Cronulla, N.S.W.

Yellowfin samples were 206 taken from the eastern Pacific Ocean in 1966, 182 taken from Hawaiian waters in 1966 and 1967, and 307 taken from waters of Line Islands in 1964 and 1967.

Genetics **59**: 79–91 May 1968.

Techniques of bleeding fish and preservation and preparation of serum and supernatant specimens were the same as those described elsewhere (FUJINO and KANG 1968).

Skipjack and yellowfin specimens representing different transferrin phenotypes were exchanged between our Laboratory and the Laboratory of the Inter-American Tropical Tuna Commission to standardize identification of transferrin bands recognized in both laboratories. Phenotypic incidences obtained by BARRETT and TSUYUKI (1967, Tables 2 and 4) were cited for statistical comparison with our results.

Electrophoresis and staining: Horizontal starch-gel electrophoresis was performed at room temperature (22°–23°C), with the same buffer system and under the same electrical conditions used for serum esterase analysis (FUJINO and KANG 1968). Transferrin bands were identified by labeling with Fe^{59} sulfate, followed by preparation of radioautographs (SMITHIES and HILLER 1959) as well as staining with amido-black (SMITHIES 1955). Results of identification of transferrin bands on each of samples from more than several hundred fishes were always identical between the above two techniques.

RESULTS

Electrophoretic patterns. Through use of Fe^{59} we were able to confirm that the bands that appeared in the β-globulin location were transferrin. Three transferrin bands were recognized in skipjack tuna and yellowfin tuna and two in southern bluefin tuna. Relative mobility of these bands is shown in Figure 1. Details are described by species.

Skipjack tuna[1]: Three bands, named 1, 2, and 3 in descending order of their mobility, occurred. These bands were identical with C, D, and E of BARRETT and TSUYUKI (1967). Five phenotypes 1-2, 2, 2-3, 3, and 1-3, were observed. A gene frequency analysis applied to all specimens taken from Hawaiian waters suggested that the six phenotypes form a system designated T_{SJ} which is determined by three codominant, autosomal alleles $T^1{}_{SJ}$, $T^2{}_{SJ}$, and $T^3{}_{SJ}$ (Table 1). A theoretically possible group, 1, was not observed among 4,366 specimens tested by us. The T_{SJ} system is independent of sex, size of fish, the blood group systems B and Y, and

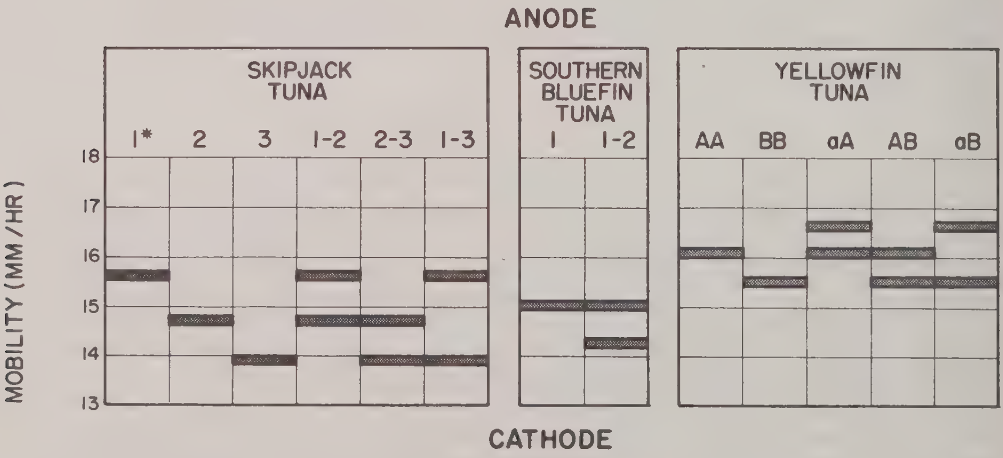

FIGURE 1.—Relative mobility of serum transferrin bands in skipjack tuna, southern bluefin tuna, and yellowfin tuna. * Not observed by us.

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[1] The nomenclature of bands and phenotypes of the transferrin system published by FUJINO (1967) was used.

TABLE 1

Comparison of observed phenotypes (O) with expected (E) in the T_{SJ} *transferrin system of skipjack tuna in Hawaiian samples*

Collected by	No. of lots		Phenotypes					Total	χ^2	Probability (2 d.f.)
			1–2	2	2–3	3	1–3			
Research vessels	18	O	11	680	598	99	5	1,393	4.51	>0.1
		E	11.8	696.3	565.3	114.8	4.8			
Commercial vessels	9	0	14	422	366	58	4	864	3.50	>0.1
		E	13.8	432.9	343.9	68.2	5.2			

serum esterase system (Sprague and Holloway 1962; Fujino and Kazama 1968; Fujino and Kang 1968).

Frequencies of genes of all 55 lots of specimens, together with data obtained by Barrett and Tsuyuki (1967) for fish from the eastern Pacific, were subjected to intra-area and inter-area heterogeneity tests (chi-square tests for contingency table). No significant intra-area and inter-area heterogeneity was present. Pooled data of phenotype and gene frequencies by area are summarized in Table 2. The ranges, means, and standard deviations of frequencies of gene T^2_{SJ} are shown in Figure 2 by geographical area. Comparison for mean values of frequency of an allele T^2_{SJ} (t-test) between neighboring areas indicated that only one combination —that between Hawaiian and eastern Pacific waters—was significantly different ($t = 2.49$, 30 d.f., $P < 0.05$). This result suggests that further data, especially from the eastern Pacific, are required to understand the relation between Ha-

TABLE 2

Phenotype and gene frequencies of T_{SJ} *system of skipjack tuna in different areas*

Area	No. of lots		Phenotypes						Total	Alleles		
			1	1–2	2	2–3	3	1–3		T^1_{SJ}	T^2_{SJ}	T^3_{SJ}
Atlantic	3	O	0	3	110	80	18	2	213	0.012	0.711	0.277
		E	0.0	3.6	107.7	83.9	16.4	1.4				
*Eastern Pacific	5	O	4	5	70	86	9	1	175	0.040	0.660	0.300
		E	0.3	9.2	76.2	69.3	15.8	4.2				
Hawaii	27	O	0	25	1,102	964	157	9	2,257	0.008	0.707	0.285
		E	0.1	25.5	1,128.2	909.6	183.3	10.3				
Japan	5	O	0	8	184	181	25	3	401	0.013	0.695	0.292
		E	0.1	7.2	193.7	162.8	34.2	3.0				
Palau	20	O	0	10	698	659	119	9	1,495	0.006	0.691	0.303
		E	0.1	12.4	713.8	626.0	137.3	5.4				

* Cited from Barrett and Tsuyuki (1967).

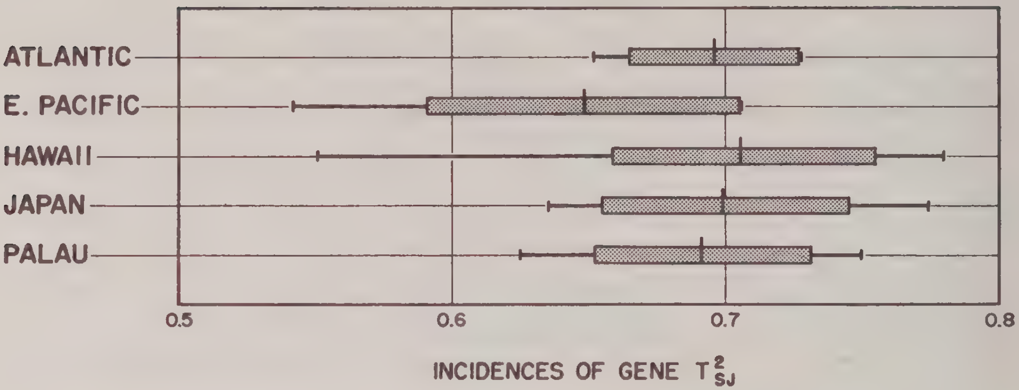

Figure 2.—Frequencies of transferrin gene T^2_{SJ} in skipjack tuna from different areas.

waiian and eastern Pacific skipjack tuna. The study of the serum esterase system (Fujino and Kang 1968) also demonstrated this need.

Southern bluefin tuna: Two bands, named 1 and 2, occurred in the southern bluefin tuna. The combinations of these bands expressed two phenotypes, 1 and 1-2, but not 2, a theoretically possible one. A gene frequency analysis shown in Table 3 suggests that the two bands are determined by two codominant, autosomal alleles of the system (T_{SB} system), T^1_{SB} and T^2_{SB}. The T_{SB} system is independent of sex and size of fish. No significant heterogeneity of gene frequencies was seen between stocks A, B, and C, which were so identified for studies of tagging and growth rate data by the staff of the Commonwealth Scientific and Industrial Research Organization (Hynd 1965; G. L. Kesteven, personal communication).

Yellowfin tuna: Two bands A and B (Barrett and Tsuyuki 1967) and another band "a" faster than A and B occurred in yellowfin tuna. The combinations of these bands expressed five phenotypes, aA, AA, AB, BB, and aB. A theoretical type aa was not observed in the 705 specimens tested. A gene frequency analysis of the transferrin system, shown in Table 4, suggests that the three recognized bands are determined by three codominant, autosomal alleles. The system is independent of sex, size of fish, and the esterase system.

TABLE 3

Gene frequency analysis of the T_{SB} *transferrin system of southern bluefin tuna*

		Phenotypes						
		1		1–2		2		
Stock*	No. of lots	O	E	O	E	O	E	Total
A	2	12	12.0	1	1.0	0	0.0	13
B	2	79	79.4	11	10.3	0	0.3	90
C	2	39	39.0	3	2.9	0	0.1	42
UI	4	137	137.6	20	18.8	0	0.6	157

* Identifications of stocks A, B, and C were provided by G. L. Kesteven (personal communication); UI—unidentified stock.

TABLE 4

Gene frequency analysis of the transferrin system of yellowfin tuna

Area	No. of lots		Phenotypes					Total	χ^2	d.f.	Probability
			aA	AA	AB	BB	aB				
Hawaii	2	O	2	99	81	9	1	192	3.05	2	>0.2
		E	2.2	102.9	73.1	13.0	0.8				
Line Is.	2	O		167	115	25		307	0.67	1	>0.3
		E		164.1	120.7	22.2					
Eastern Pacific	1	O		114	75	17		206	0.83	1	>0.3
		E		111.2	80.3	14.5					
Do.*	7	O		267	185	42		494	1.47	1	>0.2
		E		261.8	195.6	36.6					

* Cited from Barrett and Tsuyuki (1967).

Gene frequencies of the samples taken from various areas as well as results obtained by Barrett and Tsuyuki (1967) were subjected to heterogeneity tests. No significant heterogeneity was observed in either intra-area or inter-area comparisons for the eastern Pacific, Hawaii, and Line Islands.

Adaptive value of phenotypes (1) Excess of heterozygotes and deficiency of homozygotes in skipjack tuna. Comparison of the observed and expected incidences of phenotypes in Tables 1 and 2 indicates that usually an excess of phenotype 2-3 and a deficiency of phenotypes 2 and 3 existed in the samples (Table 5). For the other phenotypes, 1-2 and 1-3, no particular trend was visible. Each of the

TABLE 5

Excessive incidences of a heterozygote (2–3) of T_{SJ} *system of skipjack tuna in different areas*

Area		Phenotypes				Total	O/E ratio of 2–3 type	Hardy-Weinberg analysis	
		2	2–3	3	Others*			χ^2	P (2 d.f.)
Eastern Pacific†	O	70	86	9	10	175	1.24	8.46	<0.02‡
	E	76.2	69.3	15.8	13.7				
Hawaii	O	1,102	964	157	34	2,257	1.06	8.00	<0.02‡
	E	1,128.2	909.6	183.3	35.9				
Japan	O	184	181	25	11	401	1.11	5.01	>0.05
	E	193.7	162.8	34.2	10.3				
Palau	O	698	659	119	19	1,495	1.05	4.60	>0.1
	E	713.8	626.0	137.3	17.9				

* Sum of phenotypes 1, 1–2, and 1–3.
† Obtained by Barrett and Tsuyuki (1967).
‡ Statistically significant.

TABLE 6

Excessive incidences of a heterozygote (2–3) of T_{SJ} *system of skipjack tuna in different sexes in Hawaiian sample*

Sex	Phenotypes 2	2–3	3	Others*	Total	O/E ratios of phenotypes 2	2–3	3	Others
Male									
O	183	175	26	4	388	0.96	1.09	0.77	1.05
E	190.1	160.3	33.8	3.8	388.0				
Female									
O	195	179	24	4	402	0.95	1.11	0.75	1.00
E	204.4	161.6	32.0	4.0	402.0				

* Sum of phenotypes 1–2 and 1–3.

lots of specimens was also tested for the serum esterase system (FUJINO and KANG 1968) and they did not deviate significantly from the population from which they were drawn. Table 5 shows the observed-expected differences of phenotypes in each geographical area, although the differences do not reach the significance level of 5% for the samples from Japan and Palau. This result was seen in both sexes (Table 6).

(2) Association of phenotypic excess and deficiency with size of fish in skipjack tuna. Phenotypic excess and deficiency were examined for groups of fish of different sizes in the samples from Hawaiian waters (Table 7). Individual values and regressions of the ratio of observed/expected incidences (O/E ratio) were plotted (Figure 3). It can be seen from these relations that the phenotypic excess and

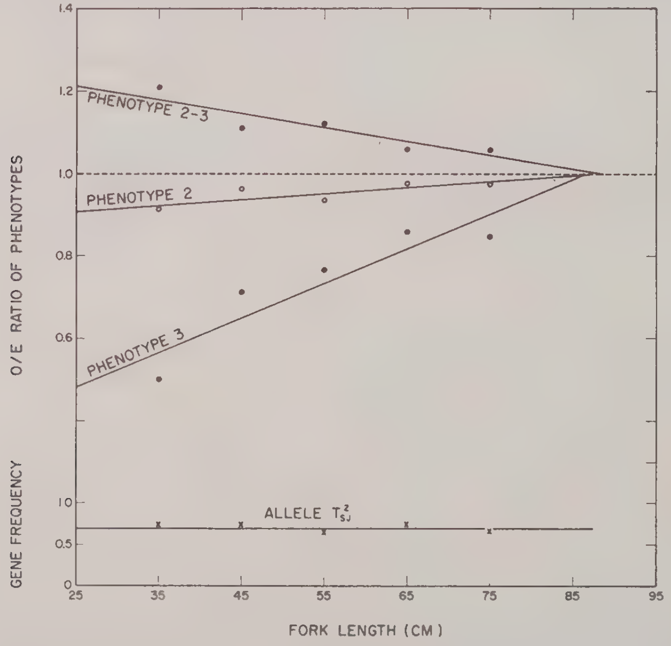

FIGURE 3.—Relation of O/E ratio of three phenotypes and frequency of allele $T^2{}_{SJ}$ of transferrin system to size of fish in Hawaiian skipjack tuna population.

TABLE 7

O/E ratio of phenotypic incidences of T_{SJ} *system in different size groups of skipjack tuna from Hawaii*

Fork length (cm)	Phenotypes										Total observed	Alleles			O/E ratios of phenotypes		
	1–2		2		2–3		3		1–3								
	O	E	O	E	O	E	O	E	O	E		T^1_{SJ}	T^2_{SJ}	T^3_{SJ}	2	2–3	3
31–40	0	0.0	21	23.0	23	19.0	2	4.0	0	0.0	46	0.000	0.707	0.392	0.91	1.21	0.50
41–50	4	3.5	201	209.3	169	152.9	20	28.0	1	1.3	395	0.006	0.728	0.266	0.96	1.11	0.71
51–60	1	0.6	60	64.3	74	65.9	13	16.9	0	0.3	148	0.003	0.659	0.338	0.93	1.12	0.77
61–70	0	0.0	58	59.5	50	47.2	8	9.3	0	0.0	116	0.000	0.716	0.284	0.97	1.06	0.86
71–80	1	1.4	38	38.8	38	35.9	7	8.3	1	0.6	85	0.012	0.676	0.312	0.98	1.06	0.84

deficiency (1) are associated with size (i.e. age) of the fish, being greater in juveniles than in adults, and (2) disappear at a fork length of approximately 86 cm, which is about the maximum for the species.

(3) Is the T_{SJ} system a balanced polymorphism? FALCONER (1961, Table 2.1 and equation 2.16) discussed the condition for balancing a polymorphism with two alleles. This can be applied to the T_{SJ} system by appropriate modification as follows.

In a system with three codominant alleles, in which the heterozygote 2-3 is overdominant and the phenotypes 1, 1-2, and 1-3 have an equal fitness, the proportionate contribution of each phenotype to the gametes that will form the next generation can be obtained, thus:

Phenotypes	1	1-2	2	2-3	3	1-3	Total
Initial frequencies	p^2	$2pq$	q^2	$2qr$	r^2	$2pr$	1
Fitness	$1-S$	$1-S$	$1-S_2$	1	$1-S_3$	$1-S$	
Gametic contribution	$p^2(1-S)$	$2pq(1-S)$	$q^2(1-S_2)$	$2qr$	$r^2(1-S_3)$	$2pr(1-S)$	A

where p, q, and r are frequencies of genes $T^1{}_{SJ}$, $T^2{}_{SJ}$, and $T^3{}_{SJ}$, respectively, in a parent population and total 1; S, S_2, and S_3 are coefficients of selection for the phenotypes 1 and 1-2 and 1-3, 2, and 3, respectively; and $A=1-S[1-(q+r)^2]-S_2q^2-S_3r^2$. Changes of gene frequencies in the next generation are:

$$\begin{aligned}\Delta p &= \frac{p}{A}\,[-S(1-p)^2+S_2q^2+S_3r^2]\\ \Delta q &= \frac{q}{A}\,[S(1-p)p-S_2(1-q)q+S_3r^2] \qquad (1)\\ \Delta r &= \frac{r}{A}\,[S(1-p)p+S_2q^2-S_3(1-r)r]\,.\end{aligned}$$

When the polymorphism is balanced, $\Delta p=\Delta q=\Delta r=0$. Then from the equations (1),

$$\frac{S_3}{S_2}=\frac{q}{r} \text{ and } \frac{S}{S_2}=\frac{q}{1-p} \qquad (2)$$

$$\text{or } S(1-p)=S_2q=S_3r, \qquad (3)$$

where $p+q+r=1$ and none of p, q, r, and A is equal to 0 or 1.

By the relation (3),

$$A=1-S. \qquad (4)$$

The phenotype frequencies in the balancing populations can be obtained from the proportionate gametic contribution, noted earlier, and equation (4) as follows:

Phenotypes	1	1-2	2	2-3	3	1-3	Total
Frequencies in population (I)	p^2	$2pq$	$q^2\frac{1-S_2}{1-S}$	$2qr\frac{1}{1-S}$	$r^2\frac{1-S_3}{1-S}$	$2pr$	1
Frequencies under no selection (II)	p^2	$2pq$	q^2	$2qr$	r^2	$2pr$	1

Ratio I/II	1	1	$\frac{1-S_2}{1-S}$	$\frac{1}{1-S}$	$\frac{1-S_3}{1-S}$	1
Ratio I/II × $(1-S)$ (=fitness)	$1-S$	$1-S$	$1-S_2$	1	$1-S_3$	$1-S$

where the frequencies I and II are represented by the observed and expected incidences of phenotypes, noted earlier, respectively. Thus fitness of each phenotype can be given as a proportion of ratio of observed/expected incidences (O/E ratio) of each phenotype against O/E ratio of the 2–3 type.

Table 8 summarizes the products of coefficient of selection and gene frequency which are defined by each term of equation (3). Values of fitness (or coefficient of selection) were calculated, as demonstrated above, from O/E ratios shown in Table 5. In Table 8, it is shown that the relations of equation (3) are satisfied except the figures of $S(1-p)$ in each area; the deviation in the figures of $S(1-p)$ seems due to low frequencies of 1–2 and 1–3 phenotypes.

(4) Unchanged gene frequency of T_{SJ} transferrin system in skipjack tuna. Equations (1) through (4) are also applicable for the life-span of a single generation of a population by replacing S, S_2, and S_3 with coefficients of mortality M, M_2, and M_3 for the phenotypes 1–2 and 1–3, 2, and 3, respectively. Then the condition by which gene frequencies remain unchanged regardless of increasing age is,

$$M(1-p) = M_2 q = M_3 r \tag{5}$$

$$\text{or } M : M_2 : M_3 = \frac{1}{1-p} : \frac{1}{q} : \frac{1}{r} \tag{6}$$

where coefficient of mortality is defined as 1 minus survival value, which is proportionate survival rate for each phenotype (where survival value of 2–3 type = 1) at given age of fish. Survival value of each phenotype in relation to the size of fish can be defined in a similar way as obtaining fitness from O/E ratio as demonstrated in section (3). Figure 4 shows the survival value-length relations obtained from the O/E ratio regressions (Figure 3). The applicability of the portion of these curves below 25 cm fork length requires verification.

If the regression of the survival value for each phenotype is actually represented by a straight line throughout the fish's life, as shown in Figure 4, the ratio $M : M_2 : M_3$ has a set of constant values, despite changes of individual values of M, M_2, and M_3 with increasing size of fish.

TABLE 8

Relative fitness of phenotypes and products of coefficient of selection and gene frequency

		Fitness			Product	
Area	$1-S$	$1-S_2$	$1-S_3$	$(1-p)S$	$q.S_2$	$r.S_3$
Eastern Pacific	0.59	0.74	0.46	0.39	0.17	0.16
Hawaii	0.89	0.92	0.81	0.11	0.06	0.05
Japan	0.96	0.85	0.66	0.04	0.10	0.10
Palau	1.00	0.92	0.82	0.00	0.06	0.05

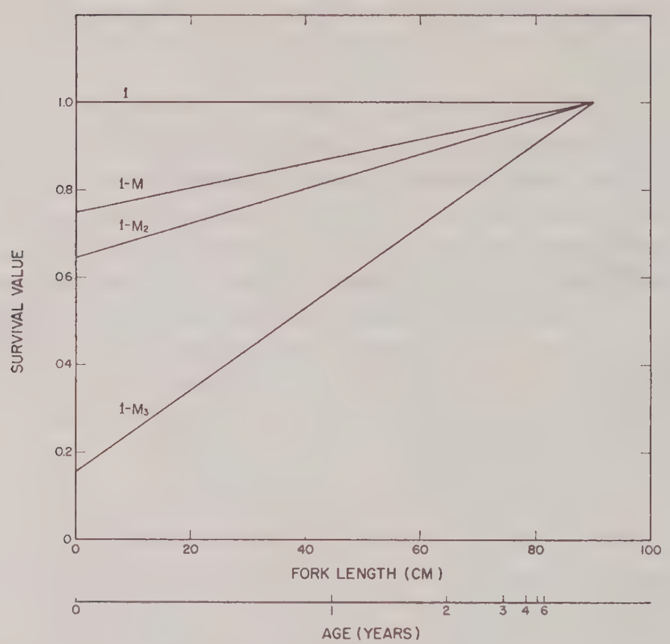

FIGURE 4.—Survival values of phenotypes of T_{SJ} system in relation to size of fish in Hawaiian skipjack tuna population. Ages were estimated from VON BERTALANFFY growth curve (ROTHSCHILD 1966).

It can be said from the above discussion, the equation (6), and $p+q+r=1$ that the condition that a set of gene frequencies p, q, and r remains unchanged throughout the life of fish is satisfied if the regression of the survival value with respect to size of fish is represented by a straight line for each phenotype.

The theoretical conclusions above were supported by the data as follows: (a) Table 9 summarizes product of coefficient of mortality and gene frequency, which is represented by the equation (5), in different size groups in Hawaiian samples. (Owing to low incidences of the phenotypes 1–2 and 1–3, the figure for the first term of formula (5) is not shown.) This table shows that the relation of formula (5) is satisfied in each size group. (b) The observed gene frequencies of Table 7

TABLE 9

Products of coefficient of mortality and gene frequency in different size groups in Hawaiian population

Fork length (cm)	Product	
	$q.M_2$	$r.M_3$
31–40	0.18	0.23
41–50	0.09	0.09
51–60	0.11	0.11
61–70	0.06	0.05
71–80	0.05	0.06

and a regression line of frequency of allele T^2_{SJ} of Figure 3 show the unchanged gene frequencies throughout different size groups.

The four kinds of evidence presented above suggest that (1) adaptive values of phenotypes exist throughout the life of skipjack tuna, (2) the survival values of phenotypes shift with age of fish, and (3) the transferrin system of skipjack tuna is a balanced polymorphism despite existence of adaptive value among phenotypes.

HYPOTHESIS ON MECHANISMS OF MAINTAINING TRANSFERRIN POLYMORPHISM

The results of the above observations and analyses now make it possible to propose a hypothesis with respect to mechanisms of maintaining transferrin polymorphism in a randomly mating population of skipjack tuna. (1) There is a significant differential fertility among different phenotypes in the T_{SJ} system, resulting in excess production of heterozygote 2–3 and deficiency of homozygotes 2 and 3. (2) These biases in phenotypic incidence at the time of fertilization are gradually compensated by differential viabilities among phenotypes with increasing age, and disappear when the fish reach their maximum size. Gene frequencies remain unchanged despite the selective pressures on phenotypes.

To test the hypothesis, 1) an extensive accumulation of data of phenotype frequency for the phenotypes 1–2 and 1–3, 2) verification of applicability of regression of survival value under 25 cm fork length of fish, and 3) an experiment of artificial fertilization (KUME 1962) by rearing fish in captivity (MAGNUSON 1965) are suggested.

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SUMMARY

Transferrin polymorphism was found in skipjack tuna, southern bluefin tuna, and yellowfin tuna taken from the Pacific and Atlantic Oceans. No significant heterogeneity of gene frequency distribution was seen between different geographical areas or different stocks in each species. Evidence for differential fertility and viability among transferrin phenotypes of skipjack tuna and their association with age of fish were described. A hypothesis on mechanisms maintaining transferrin polymorphism in a randomly mating skipjack tuna population was proposed.

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The Y System of Skipjack Tuna Blood Groups

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Summary. A blood group, called the Y system and independent of the B blood group system and of sex and size of fish, was discovered in the skipjack tuna (*Katsuwonus pelamis*). Seven reagents determine 15 phenotypes, which can be compiled into three major groups. The system was applied to population study of the samples taken from Hawaiian waters during the spring of 1965. Gene frequencies for some samples appeared to be different from those of other samples, but statistical analysis failed to demonstrate a significant heterogeneity. An extensive collection of population data was suggested to delineate exactly the population structure in Hawaiian waters.

An excellent review of the literature on blood typing of aquatic animals is found in CUSHING [4].

CUSHING [1, 2] initiated some of the first serological studies of marine fishes, including the skipjack tuna (*Katsuwonus pelamis*), a commercially important species in tuna fisheries of the world. He [3] found individual differences in red blood cell antigens of skipjack tuna, thus opening the way for studies of subpopulations of the species. SPRAGUE and HOLLOWAY [8], using reagents from normal and immune sera and saline extracts of the seeds of a species of the legume *Virgillia* on more than 1000 specimens of skipjack tuna blood collected from Hawaii, the Marquesas, Tuamotu, and Society Islands, found significant differences in the frequency of the three phenotypes of the B system of blood groups. These differences they interpreted as evidence of the existence of at least three reproductively isolated populations of skipjack tuna in the central Pacific Ocean. MARR and SPRAGUE [6] assessed the merits of the use of blood groups as one of the methods for delineating subpopulations of marine fishes.

The present paper describes a new blood group system, called the

Y system, in the skipjack tuna, and discusses the application of the system to the study of the population of the species in Hawaiian waters.

Materials and Methods

Tuna blood. Fifteen lots of blood from 2117 specimens of Hawaiian skipjack tuna were taken on the Laboratory's research vessel CHARLES H. GILBERT between April 20 and May 12, 1965. Blood specimens were taken by cardiac puncture with a syringe. Most were taken within 1 h of capture. Two techniques of preservation were employed. When the samples were to be examined within 2 or 3 weeks, they were mixed with modified Alsever's solution containing 16 g of trisodium-citrate, 41 g of dextrose, and 14.5 g of sodium chloride per 2 liters of water. A ratio of this solution to blood as low as 1:10 will suffice to preserve the specimens, but to allow for some leakage, in standard practice the ratio was set at more nearly 1:2. These specimens were refrigerated at 10°C or below, but not frozen. When the specimen needed to be preserved more than 2 or 3 weeks, it was kept frozen in an anticoagulant glycerol solution at a temperature of –15°C or below [5]. Erythrocytes were recovered by dialyzing against 1.5% saline through cellophane tubing. After being washed in the modified Alsever's solution two or three times, the cells were used for immunological analyses.

Reagents. Blood typing reagents were prepared by absorbing immune rabbit sera with skipjack tuna blood cells. Each rabbit was injected intraperitoneally five or six times with 2 ml of 50% cell suspension. Immune sera, diluted 1:4 or 1:8 with Alsever's solution, were mixed with one-half their volume of packed skipjack tuna erythrocytes and placed in a refrigerator. The packed cells were renewed three times. Time needed for each absorption was 10 to 30 min. The reagents and unabsorbed immune antisera were preserved by freezing at –15°C without any additive.

Typing blood. Agglutination tests were conducted in capillary tubes at room temperature (22°–23°C). To reach the maximum intensity of reaction, the capillary tubes were inverted almost vertically at least twice during 1 h until the final reading was made. Occasionally, test-tube agglutination tests were substituted to check the results given by capillary tubes. Throughout the serological experiments, modified Alsever's solution was used as a medium.

Serology and Genetics

Three groups, Y, YSO, and SO, were observed; these groups gave positive (+) and negative (–) reactions of + –, + +, and – + with the two reagents, anti-Y_2 and anti-$S_3(O_3)$. An additional group (– –) which is theoretically possible, has not been found in 1193 specimens tested. (Examples of agglutinin titer of the two reagents against several of the phenotypes are shown in Table VI together with those of the other five subtyping reagents described later. Here the intensities of positive agglutination reactions were rated according to an arbitrary scale running from one to four, the weakest through the strongest reactions.)

On the basis of these serological observations, the two codominant alleles, Y^{y} and Y^{so}, were proposed to interpret the genetic relationships of the blood factors Y and SO. Then three genotypes, Y^{y}/Y^{y}, Y^{y}/Y^{so}, and Y^{so}/Y^{so}, are possible for the Y, YSO, and SO groups, respectively. Under this hypothesis, Hardy-Weinberg analysis was applied to individual lots of specimens, as shown in Table I. Expec-

TABLE I

Hardy-Weinberg analysis for groups of Y, YSO, and SO of the Y blood groups in skipjack tuna

Lot	Number of blood specimens examined[1]	Blood groups Y obs.	 exp.	 YSO obs.	 exp.	 SO obs.	 exp.	χ^2	Probability 1 df
1	17	2	2.1	8	7.8	7	7.1	0.011	> 0.9
2	272	13	12.8	92	92.5	167	166.7	0.006	> 0.9
3	56	4	3.5	20	21.0	32	31.5	0.127	> 0.7
4	30	1	1.4	11	10.2	18	18.4	0.186	> 0.6
5	72	4	3.5	24	24.8	44	43.7	0.099	> 0.7
9	37	2	1.3	10	11.2	25	24.5	0.516	> 0.4
11	81	3	3.2	26	25.7	52	52.1	0.016	> 0.8
12	49	3	2.7	17	17.5	29	28.8	0.049	> 0.8
13	129	8	7.2	46	46.7	75	75.1	0.100	> 0.7
14	53	7	5.8	21	23.4	25	23.8	0.555	> 0.4
15	117	7	5.6	37	40.0	73	71.4	0.611	> 0.4

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[1] Taken from Hawaiian waters, CHARLES H. GILBERT cruise 81.

TABLE II

Relationships between blood group systems Y and B for a population of skipjack tuna in Hawaiian waters

Reagents of B-system		Blood groups of Y-system						
		Y		YSO		SO		Total
Anti-E	Anti-K_1	obs.	exp.	obs.	exp.	obs.	exp.	
+	–	17	13.1	82	80.8	138	143.1	237
–	+	23	26.9	165	166.2	299	293.9	487
	Total	40	40.0	247	247.0	437	437.0	724

$\chi^2 = 2.023$, 2 df $P > 0.3$

TABLE III

Incidences of Y blood group in different sexes of skipjack tuna

Blood group	Male		Female		Number of blood specimens examined
	obs.	exp.	obs.	exp.	
Y	14	15.2	16	14.8	30
YSO	86	85.2	83	83.8	169
SO	167	166.6	163	163.4	330
Total	267	267.0	262	262.0	529

$\chi^2 = 0.209$, 2 df $P > 0.9$

TABLE IV

Incidences of Y blood group in different size groups of skipjack tuna

Blood group		Fork length (cm)					
		<40	41–50	51–60	61–70	>71	Total
Y	obs.	2	14	4	6	4	30
	exp.	1.2	14.4	5.5	7.0	1.9	
YSO	obs.	9	79	27	45	9	169
	exp.	6.8	81.1	30.8	39.5	10.8	
SO	obs.	10	161	65	73	21	330
	exp.	13.2	158.4	60.1	77.2	21.1	

$\chi^2 = 6.665$, 8 df, $P > 0.5$

tations were calculated by applying the equations first given by Wiener and Vaisberg for the human MN blood group system [7, p. 77]. The good fit shown in the table was interpreted as supporting the hypothesis proposed for a system we call the Y blood group system. No apparent association of this system with the B blood group system [8] (Table II) and of the sex and size of fish (Tables III and IV) appeared.

By introducing five additional reagents, three series of subtyping relationships were formed by reagent combinations of anti-Y_1 and anti-Y_2, anti-S_1 and anti-S_2 and anti-$S_3(O_3)$, and anti-$S_3(O_3)$ and anti-O_2 and anti-O_1 (Table V). The specificity O_3 has never been fractionated from S_3. Thus the earlier three groups were subdivided into the 15 phenotypes observed regularly. Occasionally the existence of other phenotypes was suggested, but replicate tests proved these to be artifacts due to mistyping.

TABLE V

Y blood group system of the skipjack tuna

Phenotype		Reagent Anti-Y_1	Anti-Y_2	Anti-S_1	Anti-S_2	Anti-$S_3(O_3)$	Anti-O_2	Anti-O_1
Y group	Y_1	+	+	–	–	–	–	
	Y_2	–	+	–	–	–	–	
YSO group	$Y_1S_1(O_3)$	+	+	+	+	+	–	
	$Y_2S_1(O_3)$	–	+	+	+	+	–	–
	$Y_1S_1O_2$	+	+	+	+	+	+	–
	$Y_2S_1O_2$	–	+	+	+	+	+	
	$Y_1S_2O_1$	+	+	–	+	+	+	
	$Y_2S_2O_1$	–	+	–	+	+	+	
	$Y_1S_3O_1$	+	+	–	–	+	+	
	$Y_2S_3O_1$	–	+	–	–	+		
SO group	$S_1(O_3)$	–	–	+	+	+	–	
	S_1O_2	–	–	+	+	+	+	
	S_1O_1	–	–	+	+	+		
	S_2O_1	–	–	–	+	+		
	S_3O_1	–	–	–	–	+		

TABLE VI

Representative agglutinin titers of reagents of the Y blood group system in skipjack tuna

Reagent	Dilution	Phenotype						
		Y_1	Y_2	$S_1(O_3)$	S_1O_2	S_1O_1	S_2O_1	S_3O_1
Anti-Y_1	1: 4	4	–	–	–	–	–	–
	1: 8	4	–	–	–	–	–	–
	1: 16	4	–	–	–	–	–	–
	1: 32	–	–	–	–	–	–	–
Anti-Y_2	1: 32	4	4	–	–	–	–	–
	1: 64	4	4	–	–	–	–	–
	1:128	4	4	–	–	–	–	–
	1:256	–	–	–	–	–	–	–
Anti-S_1	1: 4	–	–	4	4	4	–	–
	1: 8	–	–	4	4	4	–	–
	1: 16	–	–	3	3	3	–	–
	1: 32	–	–	–	–	–	–	–
Anti-S_2	1: 8	–	–	4	4	4	4	–
	1: 16	–	–	4	4	4	4	–
	1: 32	–	–	2	4	4	2	–
	1: 64	–	–	–	–	–	–	–
Anti-$S_3(O_3)$	1: 8	–	–	4	4	4	4	4
	1: 16	–	–	4	4	4	4	2
	1: 32	–	–	2	2	4	3	2
	1: 64	–	–	–	–	–	–	–
Anti-O_2	1: 8	–	–	–	4	4	4	4
	1: 16	–	–	–	1	4	4	4
	1: 32	–	–	–	–	2	4	3
	1: 64	–	–	–	–	–	–	–
Anti-O_1	1: 4	–	–	–	–	4	4	4
	1: 8	–	–	–	–	4	4	2
	1: 16	–	–	–	–	3	4	–
	1: 32	–	–	–	–	–	2	–

On the basis of the serological and genetic observations described above, the occurrence of the 15 phenotypes in the Y system can be explained genetically by postulating the existence of 6 alleles, Y^{y1}, Y^{y2}, Y^{s1o3}, Y^{s1o2}, Y^{s2o1}, Y^{s3o1}, which determine antigen complexes Y_1Y_2, Y_2, $S_1S_2S_3(O_3)$, $S_1S_2S_3(O_3)O_2$, $S_2S_3(O_3)O_2O_1$, and $S_3(O_3)O_2O_1$, respectively. The resulting genotype-phenotype relationships are shown in Table VII. Under this hypothesis, the following

TABLE VII

Phenotype-genotype relationships of the Y blood group system in skipjack tuna

Phenotype		Genotype	Incidence
Y group	Y_1	Y^{y1}/Y^{y1}, Y^{y1}/Y^{y2}	$p^2 + 2pq$
	Y_2	Y^{y2}/Y^{y2}	q^2
YSO group	$Y_1S_1(O_3)$	Y^{y1}/Y^{s1o3}	$2pr$
	$Y_2S_1(O_3)$	Y^{y2}/Y^{s1o3}	$2qr$
	$Y_1S_1O_2$	Y^{y1}/Y^{s1o2}	$2ps$
	$Y_2S_1O_2$	Y^{y2}/Y^{s1o2}	$2qs$
	$Y_1S_2O_1$	Y^{y1}/Y^{s2o1}	$2pt$
	$Y_2S_2O_1$	Y^{y2}/Y^{s2o1}	$2qt$
	$Y_1S_3O_1$	Y^{y1}/Y^{s3o1}	$2pu$
	$Y_2S_3O_1$	Y^{y2}/Y^{s3o1}	$2qu$
SO group	$S_1(O_3)$	Y^{s1o3}/Y^{s1o3}	r^2
	S_1O_2	Y^{s1o2}/Y^{s1o2}, Y^{s1o2}/Y^{s1o3}	$s^2 + 2rs$
	S_1O_1	Y^{s1o3}/Y^{s2o1}, Y^{s1o3}/Y^{s3o1} Y^{s1o2}/Y^{s2o1}, Y^{s1o2}/Y^{s3o1}	$2(r + s)(t + u)$
	S_2O_1	Y^{s2o1}/Y^{s2o1}, Y^{s2o1}/Y^{s3o1}	$t^2 + 2tu$
	S_3O_1	Y^{s3o1}/Y^{s3o1}	u^2

equations were used to calculate gene frequencies from observed incidences of phenotypes:

$$p + q = \overline{Y} + \tfrac{1}{2}\overline{YSO}$$

$$p/q = \frac{\overline{Y_1S_1(O_3)} + \overline{Y_1S_1O_2} + \overline{Y_1S_2O_1} + \overline{Y_1S_3O_1}}{\overline{Y_2S_1(O_3)} + \overline{Y_2S_1O_2} + \overline{Y_2S_2O_1} + \overline{Y_2S_3O_1}}$$

$$r + s + t + u = \overline{SO} + \tfrac{1}{2}\overline{YSO} = 1 - p - q$$

$$r/(1 - p - q) = (\overline{Y_1S_1(O_3)} + \overline{Y_2S_1(O_3)})/\overline{YSO}$$

$$s/(1 - p - q) = (\overline{Y_1S_1O_2} + \overline{Y_2S_1O_2})/\overline{YSO}$$

$$t/(1 - p - q) = (\overline{Y_1S_2O_1} + \overline{Y_2S_2O_1})/\overline{YSO}$$

$$u/(1 - p - q) = (\overline{Y_1S_3O_1} + \overline{Y_2S_3O_1})/\overline{YSO},$$

where p, q, r, s, t, and u stand for the frequencies of alleles Y^{y1}, Y^{y2}, Y^{s1o3}, Y^{s1o2}, Y^{s2o1}, and Y^{s3o1}, respectively, and $\overline{Y}$, $\overline{YSO}$, and $\overline{SO}$ the incidences of the corresponding three major groups. These are a modification of the equations given by WIENER and VAISBERG for the human MN blood group system [7, p. 77].

Identification of Subpopulations

The Y blood group system has two outstanding merits for the investigation of subpopulations of skipjack tuna:

1. It is independent of sex and size of fish (Tables III and IV).
2. Statistical analysis of 10 pairs of reagent combinations provides information to determine whether, according to the Hardy-Weinberg law, a single population sample is in a genetic equilibrium (Fig. 1 and Table VIII).

TABLE VIII

Hardy-Weinberg analysis in 10 pairs of reagent combinations applied to Lot 2, CHARLES H. GILBERT [81]

Reaction pattern	Anti-Y_2	Anti-S_1	Anti-Y_2	Anti-S_2	Anti-Y_2	Anti-$S_3(O_3)$	Anti-Y_2	Anti-O_2	Anti-Y_2	Anti-O_1
	obs.	exp.	obs.	exp.	obs.	exp.	obs.	exp.	obs.	exp.
+ −	62	59.9	17	15.1	13	12.8	45	41.3	56	56.6
− +	124	123.2	167	165.8	167	166.7	151	151.0	128	129.2
+ +	43	44.9	88	91.0	92	92.5	60	63.4	49	47.6
− −	43	44.0	0	0.1	–	–	16	16.3	39	38.6
χ^2	0.182		0.447		0.006		0.519		0.063	
P	> 0.9		> 0.7		> 0.9		> 0.7		> 0.9	

Reaction pattern	Anti-Y_1	Anti-S_1	Anti-Y_1	Anti-S_2	Anti-Y_1	Anti-$S_3(O_3)$	Anti-Y_1	Anti-O_2	Anti-Y_1	Anti-O_1
	obs.	exp.	obs.	exp.	obs.	exp.	obs.	exp.	obs.	exp.
+ −	34	34.5	14	12.4	11	9.5	26	25.6	35	32.9
− +	143	144.2	209	208.0	212	211.1	179	178.7	154	152.5
+ +	24	23.4	44	46.1	47	49.0	32	32.4	23	25.5
− −	71	69.9	5	5.5	2	2.4	35	35.3	60	61.1
χ^2	0.050		0.352		0.389		0.014		0.414	
P	> 0.9		> 0.8		> 0.8		> 0.9		> 0.8	

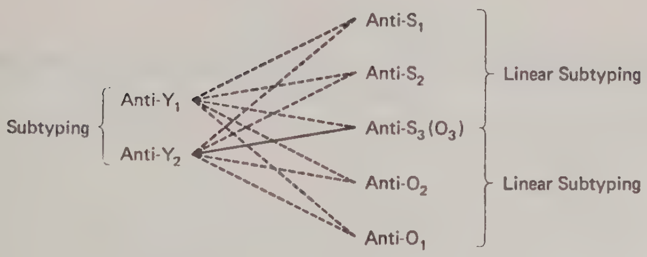

Fig. 1. Reagent combinations amenable to Hardy-Weinberg analysis of the Y blood group system. The solid line shows a combination which forms a system similar to the human MN system. The broken lines show combinations which form systems similar to the human ABO system.

Each of these principles was applied to the population study. Fifteen lots of samples came from skipjack tuna taken during cruise 81 of the research vessel CHARLES H. GILBERT. All samples were kept frozen until analyzed. They were examined 22 to 56 days after being taken. Four lots gave such a poor recovery rate of erythrocytes (35.4%) that the results of analyses were discarded. Eleven other lots gave an average yield of 68.8%.

The Hardy-Weinberg law consistently gave a good fit in 10 pairs of reagent combinations (Fig. 1) from the 11 lots. Table IX gives the frequencies of genes Y^y and Y^{so} which were calculated from Table I. Gene frequencies for the lots 1 and 14 appeared to be different from those of the other 9 lots. The heterogeneity test for the pooled data of the gene frequencies of 11 lots, however, failed to demonstrate that the heterogeneity is significant ($\chi^2 = 5.89$, 10 df, $P > 0.8$). None of the other reagent combinations of Figure 1 demonstrated any significant heterogeneity for the pooled data of the 11 lots.

Table X summarizes the observed and expected incidences of the 15 phenotypes for the six lots from cruise 81 in which only regular phenotypes were observed. The genotype-phenotype relationships shown in Table VII were used to calculate the expected incidences. Table XI gives the frequencies of the six genes for Hawaiian skipjack tuna population as calculated from the equation set out earlier. Significant inconsistencies between the observed and the expected incidences of subtypes in SO group but not in Y and YSO groups, shown in Table X, are discussed in the following section.

TABLE IX

Frequencies of determinant genes of major groups in samples of the Hawaiian skipjack tuna population

Lot	Genes	
	Y^y	Y^{so}
1	0.353	0.647
2	0.217	0.783
3	0.250	0.750
4	0.216	0.784
5	0.222	0.778
9	0.189	0.811
11	0.198	0.802
12	0.234	0.766
13	0.237	0.763
14	0.330	0.670
15	0.218	0.782

Mean and standard dev. 0.242 ± 0.050; 0.758 ± 0.050.

Comments on Technical and Biological Problems

Two technical aspects of some general and specific interest arose in the course of this study, and certain biological implications emerge from the results.

Preservation of erythrocytes. As was mentioned earlier, some of our samples were frozen. Our experience suggested that this technique maintains skipjack tuna erythrocytes in good condition for at least 2 months. Poor recovery of erythrocytes from samples that had been frozen seemed to be due more to inappropriate handling at the time of bleeding rather than to freezing. For a discussion of proper methods of taking and preserving samples, see FUJINO [5].

Accuracy of blood typing. Specificity was the same for refrigerated fresh cells and cells preserved by freezing. The cells preserved by freezing, however, sometimes gave a lower agglutinin titer against an identical reagent than did refrigerated cells. Since most of the reagents we have produced do not have high titer, as shown in Table VI, some mistyping might occur, particularly in subtyping, in extensive routine tests.

TABLE X

Incidences of 15 phenotypes of the Y blood group system for the Hawaiian population

Number of blood specimens examined		15 Phenotypes														
		Y group		YSO group								SO group				
		Y_1	Y_2	$Y_1S_1(O_3)$	$Y_2S_1(O_3)$	$Y_1S_1O_2$	$Y_2S_1O_2$	$Y_1S_2O_1$	$Y_2S_2O_1$	$Y_1S_3O_1$	$Y_2S_3O_1$	$S_1(O_3)$	S_1O_2	S_1O_1	S_2O_1	O_3O_1
414	obs.	22	4	28	26	11	6	40	22	7	5	10	51	144	36	2
	exp.	19.5	3.9	33.2	22.8	10.4	7.2	38.0	26.2	7.4	5.0	33.4	24.2	120.1	61.0	1.7

TABLE XI

Gene frequencies in the Hawaiian skipjack tuna population

Number of blood specimens examined	Six genes					
	Y^{y1}	Y^{y2}	Y^{s1o3}	Y^{s1o2}	Y^{s2o1}	Y^{s3o1}
414	0.141	0.097	0.284	0.089	0.326	0.063

Our statistical analysis (Table X) suggested that mistyping within each series of linear subtypic specificities S and O in the SO group but not in the YSO group was caused by mixed specificities in the anti-S_1 and anti-O_2 reagents; these mixed specificities seem related to the Y blood group system. This view is supported by more recent data, in which the above inconsistency almost disappeared (FUJINO and KAZAMA, unpublished data). Although incidences of the major three groups have hardly been affected by mistyping due to these subtyping reagents, it will be important to produce a higher titer of subtyping reagents to identify small differences in genetic compositions between different subpopulations.

Identification of subpopulations. Despite an apparent difference of frequencies of genes Y^{y} and Y^{so}, a heterogeneity test for the pooled data of the gene frequencies failed to demonstrate that heterogeneity was significant. Since the samples were taken within a limited span of time and range of space, the possibilities of the existence of a single population in which a genetic cline exists or of two or more subpopulations whose genetic compositions closely resemble each other cannot be ruled out. If the latter possibility exists, an extensive collection of population data is needed to demonstrate the existence of these subpopulations.

Acknowledgements

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Field techniques[1]

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SUMMARY

Variation in kinds, size, mobility, abundance, and distribution of marine zooplankton precludes use of the same sampler and methodology for all purposes. This discussion covers samplers and towing procedures in common use today; associated gear; methods required to place samplers at the desired depth, to determine depth and path of tow, and to estimate the quantity of water filtered; and care of sampling equipment. Particular stress is placed on standardization of technique to reduce variability imposed by sampling procedure.

INTRODUCTION

The term 'field techniques' is defined here as methods and procedures for operating plankton samplers. In the introductory chapter, Fraser traces the history of the development of plankton samplers and sampling methods; these were described in more detail in recent reviews by Aron (1962*b*), Currie (1962), Yentsch *et al.* (1962), Omaly (1966), and Linger (unpublished manuscript, 1960).

Most of the samplers were designed by biologists for specific objectives, and have met with varying degrees of success and acceptance. Unfortunately, not much is known about gear efficiency, and general use of a device is usually based on convenience and the premise that 'it appears to do a better job than others'. Limited studies on selected characteristics of a few samplers have been conducted ashore and at sea, but until much more definitive data on their field performance are available, a rating for them cannot be given.

Our discussion covers the samplers and towing procedures in common use today; associated gear; and methods required to place the samplers at the desired depth, to determine depth and path of tow, and to estimate the quantity of water filtered. We also comment on care of sampling equipment.

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LOW-SPEED SAMPLING

Simple net tow

The simplest arrangement for sampling zooplankton is a near-surface tow with a cone-shaped net affixed to a rigid ring, which is attached by bridles to a towing warp. This net is essentially the one Fraser describes in Chapter 1 as first used in the mid-1800's. Towing speed is generally less than 3 knots, and a weight attached to the end of the towing cable keeps the net below the surface. The net may be visible from the towing vessel and its depth known; sampling time and speed can be closely controlled. This net may also be used for vertical and oblique tows. In a vertical tow, the vessel is stopped, the weight is attached below the cod-end, the net is lowered to desired depth, cod-end first, and then is retrieved—the net fishes only on the way up. In an oblique tow, the vessel runs at low speed, sufficient cable is paid out to allow the net to sink to desired depth and the net is then slowly retrieved. Care must be taken to prevent the cable from paying out so rapidly that it slackens and kinks or entangles the net.

Modifications for subsurface towing

Modification of the simple net and weight arrangement described above is required to obtain samples from subsurface waters without contamination by material from the upper layers. The approaches used range from messenger-operated throttling devices, for taking one sample, to more complex equipment, triggered either hydrostatically or electrically, for taking multiple collections from several depths during a single tow.

Single net, mouth closure. Of the single net closing systems, that of throttling the net is the most widely used. The Nansen system, in wide use today, was first described by Gran (1905). Variations of the original design were described by Murray and Hjort (1912), Nansen (1915), Ostenfeld and Jespersen (1924), Kemp and Hardy (1929), Hentschel (1932), and Künné (1933). Basically, the Nansen net is a conical silk net with a canvas sleeve below the net ring and a noose line strung through a series of rings encircling the lower portion of the sleeve. When a messenger-operated hook releases the towing line, the strain is transferred to the noose line, throttling the net just below the mouth. Variations of the design include replacement of the canvas sleeve with open mesh netting to reduce water resistance; modification of the messenger-activated, single-action closing mechanism to permit opening and closing actions (Murray and Hjort, 1912; Kemp and Hardy, 1929; Leavitt, 1938; Motoda, 1959; Niskin and Jones, 1963); internal throttling of the net (Kemp and Hardy, 1929; Marr, 1940); and changes in location of the throttling point on the net. Throttling should be accomplished (especially in vertical tows) without permitting the net to fall backward through the water, to prevent backflow and loss of material from the mouth.

Opening and closing operations in the Nansen system were initiated by messengers or weights sliding down the towing cable to the tripping mechanism at the net, or by tripping ropes leading from the vessel to the net. The cables for a throttling system create a hazard to successful operation of the opening and closing actions, and care must be taken during launching to prevent tangling the gear. Tripping is not always reliable, and other systems have been devised for closing and opening operations. A solenoid-activated release, powered through a two-conductor rubber-covered cable, was described by Van Cleve (1937). The mechanism is cocked with the net in the collapsed position; at first release the net is opened, and at second release the net is closed by the noose rope. Opening-closing actions which are pressure operated at preset depths were described by Yentsch *et al.* (1962).

The Clarke-Bumpus sampler (Clarke and Bumpus, 1950) has a messenger-activated, spring-loaded, disc-closing mechanism. It can be attached to the wire at any point, and a series of samplers can be tripped on a single cable. This sampler has been widely used in studying vertical distribution of organisms. Improvements in its design and increase in size have been described by Paquette and Frolander (1957), Paquette, Scott, and Sund (1961), and Tranter (1965). Yentsch *et al.* (1962) described a pressure-operated opening-closing mechanism.

Single net, cod-end closure. Cod-end closure of a single net has been a recent development. Barham (1958) described a cod-end device consisting of an open-end box, equipped with butterfly valves activated in sequence by a propeller mechanism. Yentsch *et al.* (1962) described an electrically fired, explosive squib-controlled unit for meter nets. Foxton's device for large plankton nets and midwater trawls is an inverted Y-tube with spring-loaded flap at the crotch which divides the catch into two parts (Foxton, 1963). Aron *et al.* (1964) described several cod-end opening and closing devices. The most recently developed model is a tube with four chambers and four sets of doors, the doors being closed in order from rear to front by an electrical impulse through a single-conductor cable (which serves also as a towing cable), separating the catch into four discrete samples. Pearcy and Hubbard (1964) adapted the multiple net sampler described by Bé (1962) to serve as a multiple cod-end sampler for the Isaacs-Kidd midwater trawl (Isaacs and Kidd, 1953).

Recently, Longhurst *et al.* (1966) described a filtering mechanism similar to that employed in the Hardy continuous plankton recorder (Hardy, 1936*a*) to be used as a cod-end device on a half-metre net. Discrete samples are obtained as the filtering gauze is advanced in steps rather than continuously as in the Hardy sampler. Electrical drives are powered through a self-contained power supply. This device does not crush organisms as badly as does the Hardy recorder, and it can be used with a net which filters a much larger volume of water.

Multiple net sampler. Probably the most widely used multiple net system is that described by Bé *et al.* (1959) for vertical tows. In the initial design messenger-activated pivoting rods presented three previously folded nets in sequence to the flow. The first net is folded out of the way and closed as the second net is unfolded to the flow, and so on. This sampler was subsequently modified for horizontal towing, so that it can be opened and closed by a pressure-activated piston-type release mechanism (Bé, 1962).

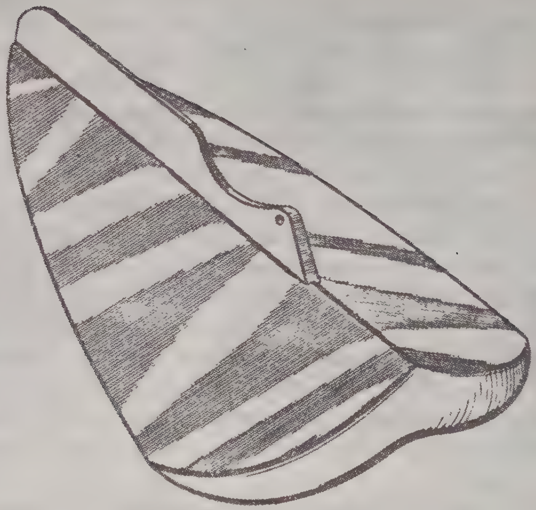

Figure 1
Scripps cable depressor
(from Isaacs, 1953).

HIGH-SPEED SAMPLING

High-speed samplers have been developed mainly because of the assumptions that tows at high speed take more representative catches of mobile organisms, and that costs are reduced by sampling at or near the ship's cruising speed. Comparative data on catch of high- and low-speed samplers are meagre and the validity of the assumption of better catching power of high-speed samplers is questionable. Of considerable merit, however, is the second aspect. Reduction in time necessary to cover a sampling grid can represent a significant saving of money and man-hours.

High-speed samplers

High-speed plankton samplers can be divided into three groups; those without, and those with opening-closing devices, and those which separate portions of the sample.

Samplers without closing devices include: a group with small mouth aperture (12 to 50 mm diameter) represented by several versions of the Hardy indicator (Arnold, 1952; Glover, 1953, 1961; Ahlstrom *et al.,* 1958; Miller, 1961); two with medium-sized mouth apertures (90 to 115 mm diameter), the Icelandic high-speed sampler (Jakob Jakobsson, personal communication), and the Jet net (Clarke, 1964); and several designs with large mouth diameters (200 to 485 mm diameter), based on the Gulf III (Gehringer, 1952; Bridger, 1958; Beverton and Tungate, manuscript). The Jet net and the Gulf III may be fitted with flowmeters.

High-speed samplers with closing devices are: the Bary catcher (Bary *et al.,* 1958) and two samplers based on the Gulf III. Bary (personal communication)

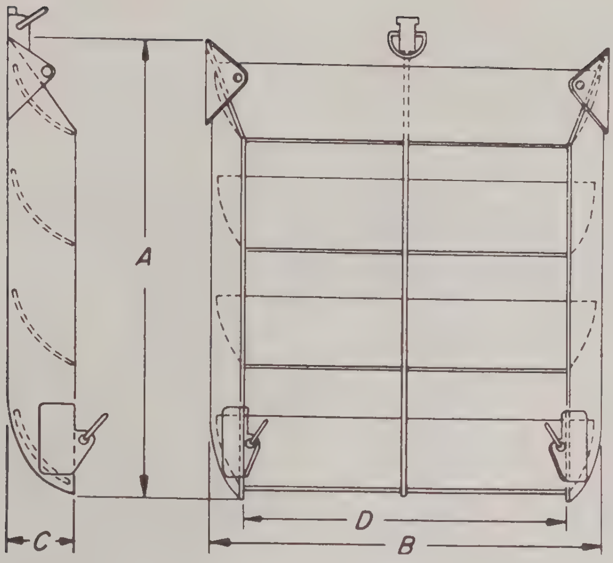

Figure 2
Multiplane kite-otter depressor
(from Colton, 1959).

U.S. Navy No.	Weight	Approximate tow load			Dimensions			
		5k	7k	10k	A	B	C	D
	(lb.)	(lb.)	(lb.)	(lb.)				
1	500	3 800		14 000	5′5¾″	5′2½″	9″	4′3½″
4	180	2 600		6 000	3′10½″	3′8″	6⅞″	3′0¼″
5	60	800	1 800	3 000	3′0¾″	2′10¼″	5″	2′4″

replaced the sleeve valve in the original version of the Bary catcher with a closing disc as in the Clarke-Bumpus sampler. A limitation is that water pressure interferes with closure of the disc at high speeds in samplers with large mouth apertures. A German version of the Gulf III, the 'Hai', has a messenger-triggered, spring-loaded lid closure that covers the nose aperture (Kinzer, 1962 and 1966); and a recent development by the Fisheries Laboratory, Lowestoft, England, uses Bé's technique of changing filtering nets (Derek Harding, personal communication). Bary's catcher and some versions of the Gulf III are fitted with flowmeters.

The third group of high-speed samplers includes those which take a series of discrete samples or a continuous sample. Neither of the samplers for taking multiple samples (Motoda, 1959; Williamson, 1963) has been widely used, but the Hardy continuous plankton recorder (Hardy, 1936*a*) has been routinely operated from merchant ships in the course of their normal business. The Hardy recorder takes a continuous sample as a propeller drive winds a band of gauze across the flow of water on to a storage spool in a preservation chamber. A closing device is not needed. A measure of water volume filtered is provided. Recently, Glover (1967) presented a proposal for the design and development of a general oceanographic vehicle, based on the Hardy recorder, which would undulate vertically in the upper

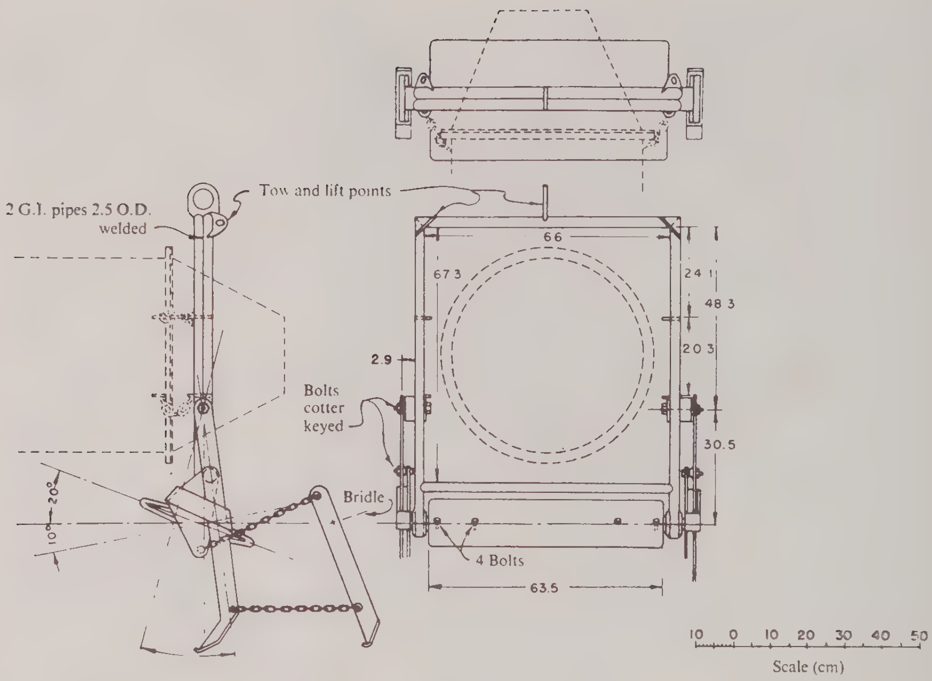

Figure 3
Boothbay depressor No. 3 (from Graham and Vaughan, 1966).

100 metres as it is towed at normal cruising speeds, and would record physical variables as well as sample the plankton.

Special problems of high-speed sampling

Increased drag of samplers and towing cable in high-speed towing introduces special problems. Dead weights, streamlined or not, are the only suitable means of taking a net to depth in vertical hauls and other tows at speeds below about 3 knots. They have the advantages of simplicity, ruggedness, and low cost. The weight required to attain depth at higher speeds, however, is large enough to cause serious handling problems, and to become hazardous during rough weather.

Depressors. The problem of attaining high depressing force without great weight has been partially solved through the evolution of hydrodynamic depressors which have high lift/drag ratio. One of the earliest depressors was a square iron plate hinged at an angle to the lower edge of the frame of the Heligoland young fish trawl (Ehrenbaum and Strodtmann, 1904). Since then hydrodynamic depressors of many kinds have been developed either as integral parts of the sampling device, as in the young fish trawl, or as separate units that can be used with a variety of towed objects.

The Scripps homogeneous depressor (Isaacs, 1953) shown in Figure 1, probably

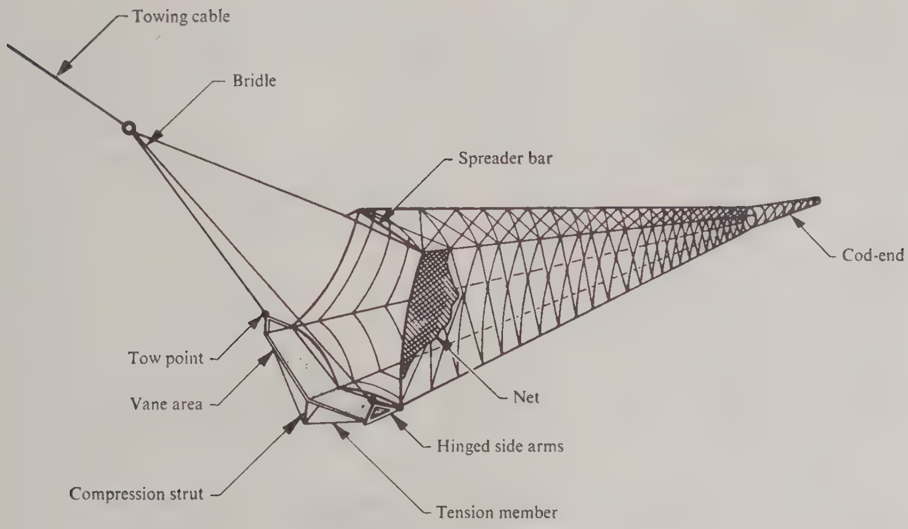

Figure 4
Isaacs-Kidd midwater trawl (from Isaacs and Kidd, 1953).

the most widely used device of this kind, has been used with the full array of samplers ranging from the Clarke-Bumpus (Clarke and Bumpus, 1950) to the Gulf III sampler (Gehringer, 1952). Less widely used are the multiplane kite-otter (Colton, 1959) of Figure 2, and the Boothbay depressor (Graham and Vaughan, 1966) of Figure 3. The latter is designed for sampling very close to the bottom and is so built that accidental contact with the bottom alters the 'angle of attack' and prevents the depressor from digging in and damaging the sampler. The V-fin, a stable low-drag depressor of hydrodynamic design, has been used in surveys with echo-sounders towed by helicopters in the Canadian Arctic (Eaton, 1963), but its value as a depressor for plankton samplers appears limited.

Of the depressors which are an integral part of the sampler, the two in widest use are blades. One is associated with the Hardy continuous plankton recorder (Hardy, 1936*a*) and the other with the Isaacs-Kidd midwater trawl (IKMT) (Isaacs and Kidd, 1953), Figure 4. Several modifications have been made to the IKMT depressor to simplify handling. Taniguchi*[1] used a Y-shaped depressor and substituted canvas for steel to reduce weight. Bercaw (1966) described a folding aluminium depressor for the 6-foot net which has proven easy to handle and to store.

Smith *et al.* (1964) described a modified version of the Gulf I-A sampler (Arnold, 1952) with trim tabs on the horizontal stabilizers, eliminating the need for an independent depressor. This sampler was towed successfully at about 2 metres depth at speeds to about 18 knots. Glover (1967) described an undulating oceanographic instrument which utilizes two depressing planes, inverted aerofoil sections of approximately the same shape and same degree of anhedral as conventional cable depressors. This instrument follows a sinusoidal tow path, achieved

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[1] Asterisked (*) references denote information presented at the Sydney Symposium.

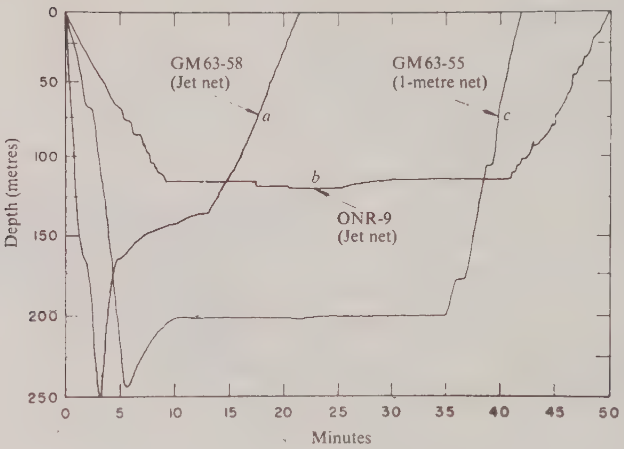

Figure 5
Tows of the Clarke Jet net and 1-metre ring net. Curve *a*, Jet net with 82 kg weight; curve *b*, Jet net with Scripps depressor, both at 4 knots; curve *c*, 1-metre ring net with 45 kg weight, at 2 knots (from Aron *et al.*, 1965).

by rotating the diving and tail planes with power taken from a propeller at the after end of the sampler.

Performance studies of depressors. Studies on field performance of depressors have been limited, primarily because instrumentation for monitoring performances has only recently become available. Aron *et al.* (1965) obtained information on the characteristics of a number of the above depressors and several sampling devices.

Hauls made with a 1-metre ring net and the Jet net (Clarke, 1964) are shown in Figure 5. Ship speed was held constant throughout these tows. When a simple weight is used for attaining depth there is a considerable decrease in sampling depth when the winch brake is set at the end of cable payout. The low lift/drag ratio of the dead-weight depressor can also be seen by comparing the two Jet net tows, one with a dead-weight (curve *a*) and one with a Scripps depressor (curve *b*). Approximately the same depth was attained in both tows with the same cable length, despite the fact that the depressor weighed only 20 kg and the dead-weight 82 kg. More important, there was no change in depth when the brake was set during the haul with the Scripps depressor.

In 5.6 knot tows with the Bary catcher (Bary *et al.*, 1958), the Scripps depressor was compared with the multiplane kite-otter (Fig. 6). The high lift/drag ratio of the kite-otter is demonstrated by its much lower ratio of cable length to depth (roughly 2:1) in comparison with the Scripps depressor (4:1). The net path was very erratic in the tow with the kite-otter, however, due to the instability of the depressor. This condition was improved by adjustment of the bridles, to which the kite-otter appears to be very sensitive. If this sensitivity can be reduced, the unit would be most useful.

Bary (personal communication) has compared the Scripps depressor and the multiplane kite-otter used with the Bary catcher. His observations indicate that: (a) the kite-otter has two to three times the down-lift of the Scripps depressor (proportionately increasing in favour of kite-otter as speed increases); (b) the kite-otter will take equipment deeper on a shorter length of warp at any one speed

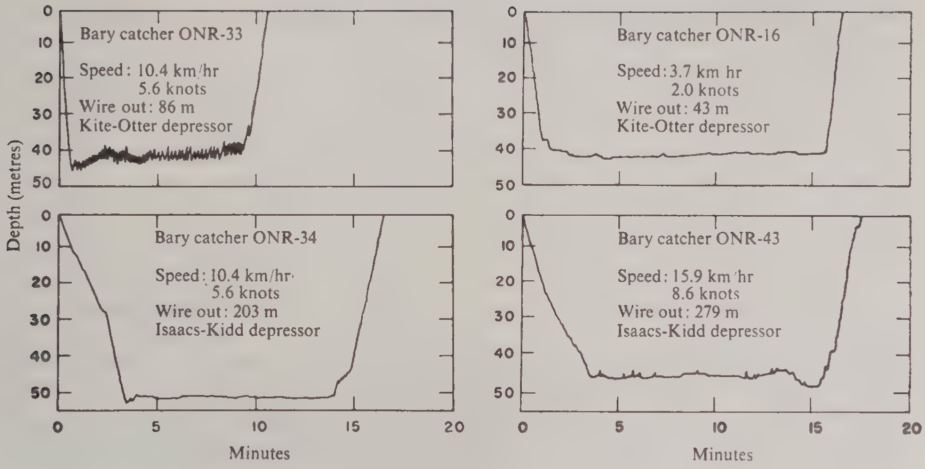

Figure 6
Bary catcher tows, showing variation in length of wire required to get same depth at various speeds (from Aron *et al.*, 1965).

and can descend to much greater depth at all speeds, but is not so convenient to use as the Scripps depressor; (c) the Scripps depressor of 45 pounds (20.4 kg) cannot overcome lift of wire ($^9/_{32}$ inch diameter) at towing speeds above approximately 6 knots for lengths of cable greater than 300 metres; and (d) both depressors show indications of instability, but at lower speeds in the kite-otter than in the Scripps depressor. Colton (1959) gave plans and performance characteristics for several models of the kite-otter depressor.

Aron *et al.* (1964, 1965) described the towing behaviour of a 6-foot IKMT, in which the depressor is an integral part of the sampler. The data for cable lengths of 100, 200, 400, 800 and 1,600 m show that sampling depth increases with decreasing towing speed, with greater effect at lower velocities. This same observation was made for all of the other depressors which were tested, and it appears to hold for depressors in general.

The dead-weight lost depth when the winch brake was set after all the cable had been paid out, the Scripps and kite-otter depressors seemed to hold depth, and the IKMT increased in depth (up to 50 per cent greater). The time required for the IKMT to attain stable towing depth generally increased with increasing wire length. In a series of hauls at 5 knots, in which towing speed was reduced to about 2.5 knots to facilitate recovery, the IKMT went deeper and for about half the recovery period was below the original depth of sampling (Table 1). Taniguchi *et al.* (1965) and Imanishi *et al.* (1965) confirm this increase in depth during recovery. They also showed that the gape height of the net at towing speeds of 5 to 7 knots was 25 to 35 per cent less than that of the stationary net. These papers also include information on the towing resistance of two 10-foot models of the IKMT relative to speed.

TABLE 1. Towing characteristics of 6-foot Isaacs-Kidd midwater trawl relative to length of wire out; towing speed 5 knots, reduced to 2.5 knots for recovery

Wire out (m)	Depth at end of pay-out (m)	Stable depth (m)	Time to stabilize (min.)	Recovery time (min.)	Time below stable depth (min.)
100	20	29	2	1.50	0.40
200	39	58	5	3.30	1.0
400	72	104	7	6.42	4.0
800	145	183	7	13.26	6.0
1 600	245	335	13	28.43	14.0

Towing characteristics of samplers. Aron *et al.* (1965) showed that the towing characteristics of the Gulf III and the Bary catcher were similar, as might be expected of nets with approximately the same dimensions and external shape, and that the Jet net also conformed, although it has considerably different proportions of length and diameter.

The towing characteristics of other samplers are poorly documented. During an oblique tow with the Bé multiple plankton sampler (Bé, 1962), the path followed by the net during payouts was highly irregular (Fig. 7). The irregularity appeared to start at the time of net opening. Data are sparse, but it might be expected that a change in the configuration of the sampler would alter the tow path, and this appears to occur during tows of the Bé sampler. This possibility and its potential effect on interpretation of data may be relevant to other opening-closing devices that change the effective cross-sectional resistance of the net to the water column. Bary has found that closing the Bary catcher has no effect on the towing path in a few monitored tows (personal communication).

DETERMINATION OF DEPTH OF SAMPLING

After length or duration of tow, depth of sampling is the parameter most often measured by planktologists. The simplest technique is to measure the length of cable in the water with a meter wheel, and the cable angle with a clinometer, and to compute the depth of sampling. This method assumes that the cable forms a straight line from the surface to the sampler. With increasing cable lengths, however, this assumption generally introduces an increasingly greater error as a catenary forms in the cable. A further error in the depth estimate may occur if changes in the angle at the surface remain undetected, or fail to occur in response to depth changes, as for the Bé sampler (Fig. 7) and the kite-otter depressor (Fig. 6).

Maximum depth and depth-distance recorders

The desire for more reliable depth information has led to the development of techniques for obtaining direct measurements. The simplest of these are the Kelvin tube and the bathythermograph which are 'maximum-depth' recorders. These instruments record the maximum depth reached during the haul, but provide no

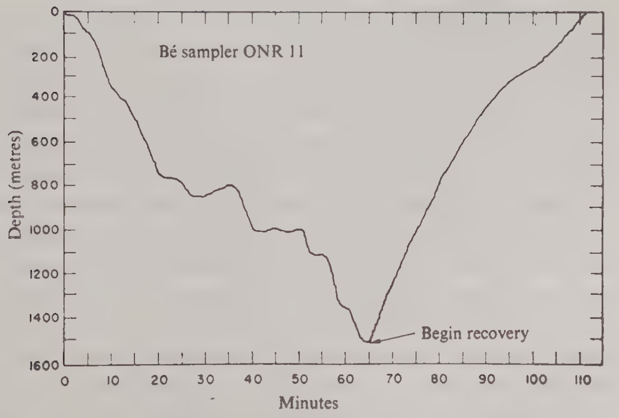

Figure 7
An oblique tow with the Bé multiple plankton sampler, at 1 knot using 45 kg weight (from Aron *et al.*, 1965).

other information on the tow path, and are generally limited to depths of 500 metres or less. Also, depth is not known until the completion of the haul.

To obtain further information on the tow path, Moore (1952) developed a depth-distance recorder. This device employs a standard bathythermograph slide moved lengthwise by a propeller-driven, worm-operated screw to record distance travelled through the water. Depth is recorded on the slide by a stylus attached to the end of a Bourdon tube. Although this device has not seen wide use, the technique probably provides the least expensive method of recording the sampling path and should not be overlooked. The integrated depth recorder (Hamon, Tranter and Heron, 1963), also used with a Bourdon tube, gives a variable density trace on a fixed photographic film by means of a radioactive source. Maximum and average depths and variation about the average can be read off.

These or other similar types of depth recorders equipped with Bourdon tubes (which can be exchanged according to depth range of operation) are in use with the Gulf III and the IKMT. In the older (but more reliable) type, the recording paper is driven by a simple clockwork motor with a watch spring; the newer type is battery driven. The rather heavy steel casing required for the depth recorder can serve as additional dead-weight.

Another simple method of recording the sampling depth has been designed by D. Brown of the Scripps Institution of Oceanography. This equipment plots depth versus time on an inexpensive battery-powered recorder. This and similar recorders available on the commercial market have been widely used.

Monitoring depth during sampling

In each of the above instruments the depth data are available only after the tow is completed. Because there are obvious advantages to knowing the sampling depth during the haul, a number of monitoring techniques have been used.

Acoustic telemetry. Backus and Hersey (1956) used an echo-sounder from a following ship to determine the cable configuration and depth of an Isaacs-Kidd midwater trawl. This procedure requires no additional special equipment, but the very considerable skill and time required limit the technique primarily to calibration tows.

Dow (1955) described an acoustic telemetering depth meter in which a hydrophone towed at the surface received a signal radiated by a transducer attached close to the plankton sampler. The NIO depth-telemeter, based on Dow's unit, consists of a self-contained transmitter, attached to the net, which measures pressure, converts it to a frequency and transmits it over an acoustic link to a hydrophone towed behind the ship (Tucker *et al.*, 1963). The accuracy achieved is within about 1 per cent of the working range; instruments with maximum depth ranges of 200 and 600 m respectively are in routine use.

Recently, Backus (personal communication) has employed a depth telemetering pinger which uses the ship's echo-sounder as a receiver. Quality of data depend upon the precision of the ship's depth recorder and the accuracy of the pressure sensor. Backus used a Precision Graphic Recorder, with greater accuracy than the average echo-sounder, and results appear to be within the accuracy specified by the manufacturer of the pressure sensor (± 3 to 5 per cent, depending upon the sensor used).

The Furuno Net-Sonde, an acoustic-telemetering depth meter, has been used principally in Japan to assist in placing a net at the same depth as fish groups. This has potential in plankton studies.

Electric telemetry. Boden *et al.* (1955) described a depth-recording unit which telemetered data along a single-conductor insulated cable to a recorder on deck. Aron *et al.* (1964) and Bourbeau *et al.* (1966) described a system for telemetering depth electrically by using a single-conductor, load-bearing electrical cable. Their use of a multiplexed FM system allows the simultaneous telemetry of data on temperature, light, and net speed, in addition to depth, and also permits the electrical control of a cod-end sampler. Other sensors can be added without changing the cable or winch requirements. In cost and reliability, the single-conductor cable closely approximates that of non-conductor cable of similar strength.

Acoustic versus electric telemetry. In the consideration of the relative merits of acoustic telemetry and telemetry through a single-conductor cable, several points should be mentioned. The initial costs of acoustic telemetry of a single variable are generally less than those of an electrical conductor system. The transmission of data simultaneously from several sensors, however, is easier, more reliable, and for most purposes less expensive electrically than acoustically. Problems of ambient noise, slant range, and variable sound velocity are eliminated by telemetering electrically. In addition, the limited rate at which information may be transmitted in acoustic telemetry, renders this approach generally unsatisfactory for use with rapidly changing variables such as bioluminescence.

MEASUREMENT OF VOLUME OF WATER FILTERED

A measure of the quantity of water filtered during a plankton tow is essential in quantitative sampling. A flowmeter mounted in the mouth of the simple conical net provides a means of estimation. Recent studies of the water velocity at various points across the mouth of the net suggest that a better estimate of the flow through the net is obtained by a meter positioned midway between the centre of the mouth and net rim, rather than centred in the mouth as is commonly done.

A second flowmeter, placed in the free stream outside the net, provides an estimate of the speed of the sampler through the water and, combined with the meter in the mouth, an estimate of the sampler's filtration efficiency. This arrangement is useful in determining the maximum length of time a net of a particular mesh size can be towed in a given body of water before it becomes clogged. Clogging reduces the filtration efficiency of a net, which affects meter readings, and in turn, estimation of the volume of water filtered. Unusually large differences in the readings between the sampler flowmeter and the free stream meter would suggest clogging, and the inaccurate estimate could be discarded. The necessity for rigid standardization of conditions from tow to tow cannot be overemphasized. Without the second meter, we can only speculate on the possibility of clogging.

The simplest flowmeters in use today indicate the number of revolutions of the impeller blades on a series of dials or on a counter. They are commonly supplied with a calibration curve from the manufacturer and are rated for speeds up to 5 knots. These meters provide information after a tow has been completed, and are probably adequate for most sampling programmes. The TSK flowmeter (Nakai, 1954) has proven to be a highly reliable and sturdy meter of the dial type. Tungate and Mummery (1965) described an inexpensive mechanical digital flowmeter. Comita and Comita (1957) described a modification of the Clarke-Bumpus sampler in which a control system can be preset for passing definite quantities of water through the sampler.

Calibration of flowmeters is best done in a testing facility where speed and distance can be closely controlled (Tranter and Smith: see Chapter 3 above). The standard field calibration method is to tow the flowmeter free of the sampler over a known distance and equate impeller revolutions to a measure of distance.

Recent developments in acoustical and electrical instrumentation have provided means of monitoring flow and other sensor data during towing. These systems require either electrical circuits between the sampler and the vessel or acoustical transmission and receiving equipment. One reason for monitoring during a tow is to determine when clogging begins, so a haul may be terminated before further clogging affects the estimate of water filtered. Several manufacturers now offer telemetering ducted impeller current meters, reported to be accurate at speeds up to 5 knots.

The validity of estimates of volume filtered obtained by a meter mounted in the exhaust of the Gulf III high-speed sampler (Gehringer, 1952) is highly questionable. Recent studies of flow velocities across the exhaust of the Gulf III revealed highly variable turbulence which makes estimates of total volume with present meters unrealistic.

There is evidence that flowmeters with impeller blades which nearly fill the mouth or exhaust of a sampler are more accurate than small flowmeters in estimating total flow.

TOWING EQUIPMENT AND PROCEDURES

Most cruises are multipurpose, and the biologist must share available winch, cable, and gear handling facilities with other programmes. These must be adequate for the heaviest gear to be operated, and probably are not best suited for handling and towing plankton gear. Adequate gear-handling facilities are essential to safety, particularly when heavy instruments are used. Figure 8 (from Beverton and Tungate, manuscript) illustrates an adequate arrangement for handling a large multipurpose plankton sampler. For any work at sea the quality of results is in part determined by the ease of operation. Since collections are often made by technicians, who have little personal interest in the results, adequate handling gear and a set of procedures to be rigidly followed should be provided.

Equipment

Winches. Oceanographic winches are subjected to gruelling conditions and are frequently overloaded. It is important to choose a winch of rugged and conservative design. Those not experienced in writing and enforcing engineering specifications would do well to deal only with manufacturers who have produced satisfactory oceanographic winches in the past, and to adhere, if possible, to proved designs. It would be well also to obtain advice and copies of specifications from an organization which has experience in procuring winches. (Many companies cannot be made to realize that winches for long wires differ from winches for short wires.) In general, careful attention should be paid to the following points.

Spools must be exceedingly rugged to avoid crushing of the core and distortion or breakage of the flanges by the many turns of wire. Good durable level-winds (spreaders) must be provided, and special thought must be given to making fair-leading devices which will not be worn excessively by the wire. Power should be adequate for long hauls without overheating the driving mechanism. The brake should be easy to apply and strong enough to break the heaviest wire which is to be used. Similarly, the winch structure, the level-wind, the fastenings to the deck, and the deck itself usually should be strong enough to break the wire without suffering damage.

The size, power requirement, and cost of a winch are determined by the choices of wire size, wire length, hauling speed, and load on the wire. The required horsepower output may be obtained by multiplying the hauling speed in feet per minute by the actual dynamic wire tension in pounds and dividing by 33,000. Since the horsepower efficiency will be only 50 to 75 per cent, the driving motor must be correspondingly larger. And, if the power sources used lack the short-term overload capacity of electric motors (e.g., some hydraulic drives, or internal combustion engines), additional power must be provided for such overloads. It is well to provide for unanticipated long-term overloads, or, more desirably, to have a gear-shift or equivalent mechanism that exchanges torque for speed, to haul heavy loads in emergencies. In estimating the working tension one should add the static pay-load, the weight of all the wire, the drag forces on wire and equipment at the hauling speed, and then multiply by a safety factor (at least 1.5) which includes effects due to surging of the ship and provision for unknown demands of the future.

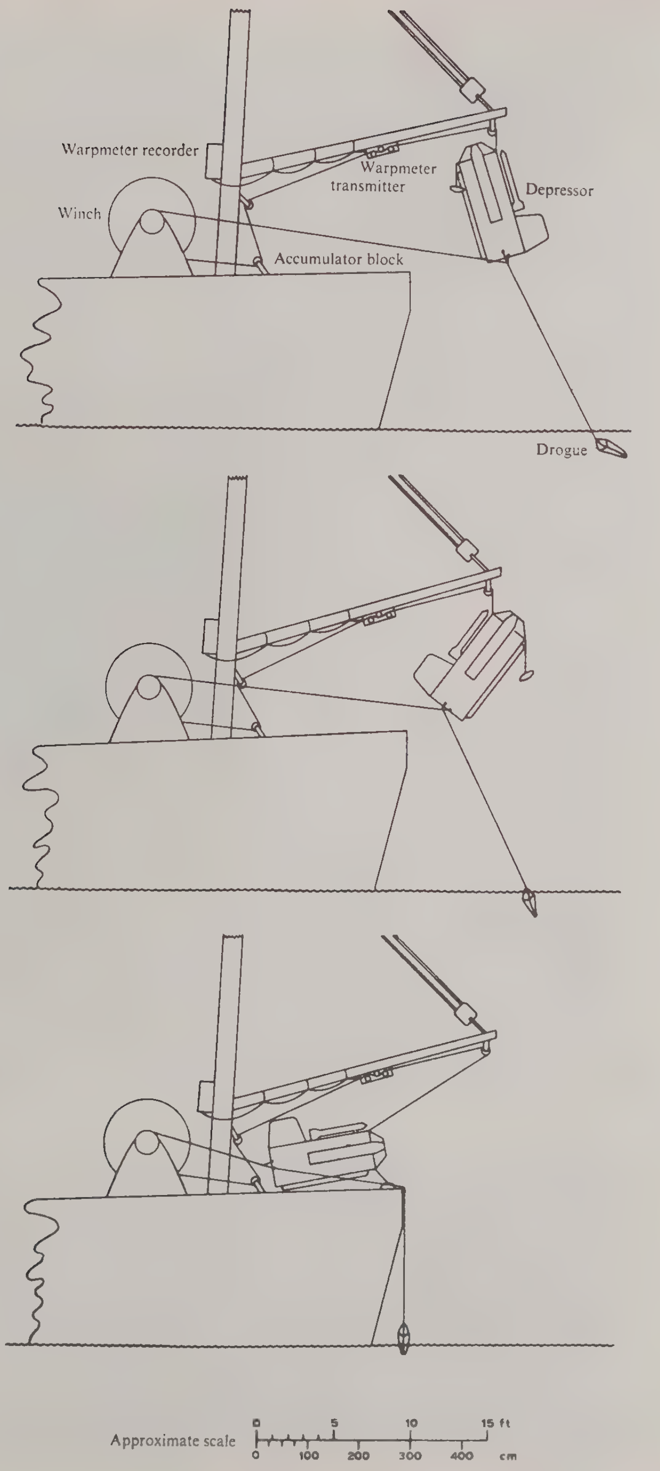
Warpmeter recorder
Warpmeter transmitter
Winch
Depressor
Accumulator block
Drogue
Approximate scale
0
5
10
15 ft
0
100
200
300
400
cm

Figure 8
Diagrammatic lay-out of winch and towing gear, and three stages of retrieving of the multiple sampler (from Beverton and Tungate).

Speed controls are important. For winches in which fine control of wire length at creeping speeds is necessary, the purchaser will be rewarded if he gives special attention to this capability. Such controls may be had with: gear shifts or their hydraulic equivalents; properly designed throttle control of a hydraulic motor; conventional armature control of an electric motor by wiring the first controller step to include a shunt across the armature; Ward-Leonard control; and thyratron control. Unmodified armature control is less satisfactory, but is often used. It works reasonably well if the number of steps on the controller is relatively large.

Cable and sheaves. The cable diameter influences the towing characteristics of samplers—large diameter cables create more drag than small ones. Colton (1959) recorded the differences between tows taken with cables of 6.4 and 12.7 mm diameter. In a report for the David Taylor Model Basin, Pode (1951) produced tables for determining the configuration and tensions of a flexible cable moving in a fluid.

The wire rope manufacturer can recommend the proper size and type of wire rope for any use. A 7 × 19 construction of stainless steel or galvanized plough steel is flexible and easy to handle and is widely used in plankton sampling. The safe working load is generally figured at one-fifth the breaking strength, but for some uses, as low as one-eighth is recommended. Certain minimum sizes of sheaves for different sizes of cables are recommended by the manufacturers of wire ropes, but whenever a larger diameter can be conveniently used, it is preferable. The total stress due to bending over a sheave may be a sizeable portion of the safe working load, and the recommendation of an engineer for a particular set of conditions is advisable. Sheaves with too small a groove shorten cable life.

During towing operations cable may be subjected to severe loadings because of large-amplitude ship motions. These motions first cause the cable to become slack and subsequently subject it to impact stresses at the instant of tension recovery. A study to establish the guidelines for minimizing the effects of slack-cable in towed-body systems is described by Schneider *et al.* (1964).

Cable fairing is useful in reducing vibration, noise, and drag. The cost and problems associated with winding will probably restrict the use of faired cable except where control of vibration, noise, and cable length are critical to operation of the sensors being towed. We have no measure of the noise created by samplers and cables during towing, nor do we know what effect reduction of the noise might have on the numbers and kinds of organisms captured.

Accumulators. Compression springs, or accumulators, have been incorporated into the boom and block rigging to take up sudden jars and minimize the effect upon the towing cable of the vessel rolling. Hensen (1895) illustrated an accumulator constructed of a number of heavy rubber bands. Most accumulators today are compression spring assemblies mounted in the topping lift of the towing boom, or spring-loaded sheaves, sometimes mounted on the deck, through which the towing cable passes from winch to towing boom. When lengths of cable are great the surge is partially absorbed through the catenary formed in the cable. A shock absorber in line between the end of the towing cable and the sampler has been used with the Hardy continuous plankton recorder (Hardy, 1936*a*) and the Gulf III sampler (Anderson and Gehringer, 1957) to reduce cable strain, vibration during towing, and surges.

Standardization of technique

It is impossible to exaggerate the importance of rigorous care in standardizing sampling technique to reduce variability imposed by the sampling procedure.

For oblique and also horizontal tows taken at any significant depth, without a closing device, the winch speed during pay-out and recovery should be regulated. For all tows ship's speed should be kept as nearly constant as possible. Variations in speed lead to variations in sampling depth. Unless suitable closing devices and depth monitoring equipment are used, data interpretation will be biased indeterminably. Further bias is introduced by avoidance in some species at low velocities and escapement at higher speeds.

It should be appreciated that net speed relative to the water column being sampled is frequently very different from ship speed. Since net speed is a significant factor in avoidance and escapement, it is strongly recommended that a flowmeter be installed outside the net. Ideally, the flowmeter should provide a continuous record of time versus velocity; however, even a simple flowmeter such as a TSK can provide a useful measure of average speed during a tow.

Care should also be taken to wash down the nets carefully after each tow. Improper washing causes contamination of samples with collections from previous tows. There is also danger, especially for the nets with finer gauze, that improper washing will hasten clogging and thus prevent the reasonable comparison of successive hauls.

During any long-term or large-scale programme which will require either the replacement of nets or the use of several nets having the same gauze, it is urged that all of the required material be purchased at the same time from the same supplier. It is common to find significant differences in netting of the same specification number, purchased at different times or places. These differences make comparison of collections difficult. Care should also be taken to examine sampling equipment routinely to ensure that ageing and use have not modified the sampling characteristics (particularly, for example, by altering the shape and size of the meshes).

Care of sampling equipment

Nets. The use of synthetic fibres has increased the life of a plankton net, but synthetic materials are subject to abrasion and some, like nylon, deteriorate in sunlight and should be stored in the dark. Silk nets should be thoroughly washed with a mild detergent and scrubbed with a soft brush and rinsed with fresh water after a cruise, or several times during long cruises. Nets of synthetic fibres should be cleaned according to the recommendations of the manufacturer. See Heron (Chapter 2 above) for a comparison of the resistance of silk and synthetic fibres to abrasion and chemicals.

A dilute solution of commercial or household bleach is effective in cleaning nylon, but it will deteriorate silk. A 5 per cent solution of hydrochloric acid brushed over monel metal netting removes clogging materials and corrosive deposits effectively, but exposure to the acid should be limited to a few minutes and the net thoroughly rinsed with fresh water. The gauze can then be examined under a hand lens to determine if a second application of acid is necessary.

Care should be taken to prevent nets from coming in contact with sharp or rough surfaces. A new net may be strong enough to stand some abrasion, but it becomes increasingly fragile with use. Gear should be thoroughly inspected before use—a weakened net may split during a sudden surge. Discarding nets of questionable strength should be standard procedure. Metal gauze is more resistant than silk or synthetic fibres, but its rigidity makes it susceptible to puncture.

Cables. Cable fatigue can result in loss of gear. It is considered good practice to discard the terminal few feet of a towing cable periodically to eliminate the portion most likely to be affected by fatigue.

Depressors. The efficiency and stability of depressors depend upon their balance. They should be launched and retrieved carefully to prevent damage which might impair their stability. Improperly balanced depressors are not efficient, and unstable depressors can become deadly projectiles if they surface and break free of the water while being towed at high speeds.

Flowmeters. Flowmeters should be checked for damage between tows. Generally, simple adjustments to tension on bearings can be made at sea, but other adjustments should be made only by trained technicians. Meters should be calibrated after repair or adjustment and all meters should be recalibrated periodically.

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Terminology

Plankton catch (x): the quantity of plankton of a particular kind taken by a plankton net.

Volume filtered (w): the volume of water filtered by a plankton net in collecting plankton from a natural body of water.

The catch per unit volume filtered (X) is given by the equation

$$X = \frac{x}{w} \cdot$$

Plankton sample: a collection of plankton that is believed to be representative of the natural body of water from which it is taken.

Plankton samples are usually biased because some plankters avoid the net (*avoidance*) and others are lost through the meshes (*escapement*). An estimate ($\hat{y}$) of the number of plankters of a particular kind in an unbiased sample is given by the equation

$$\hat{y} = \frac{x}{C \cdot S}$$

where S is the *mesh selectivity* of the net, and C is the *catching efficiency* of the sampler of which the net is a part.

Plankton concentration (Y): the quantity of plankton of a particular kind per unit volume of a natural body of water. An estimate ($\hat{Y}$) of the plankton concentration is given by the equation:

$$\hat{Y} = \frac{\hat{y}}{w},$$

the accuracy of the estimate depending not only on the sampling bias, but also on the plankton distribution within the water body.

Filtration efficiency (F): the ratio of the volume of water filtered by a plankton sampler to the volume swept by the sampler mouth. That is,

$$F = \frac{w}{A \cdot D} \tag{a}$$

where A is the mouth area of the sampler and D is the distance towed. The relation may also be expressed as:

$$F = \frac{A' \cdot D}{A \cdot D} = \frac{A'}{A} \tag{b}$$

where A' is the *effective mouth area,* or as:

$$F = \frac{A \cdot V'}{A \cdot V} = \frac{V'}{V} \tag{c}$$

where V is the towing velocity, and V' is the mean velocity of the flow through the sampler mouth.

Mesh: one of the open spaces (pores) in a net, enclosed by the strands of a meshwork which may be termed the *gauze.*

Porosity (β): the open area fraction of the gauze comprising the filtering surface; β may be calculated from the equation:

$$\beta = \frac{m^2}{(d + m)^2}$$

where m is the *mesh width* and d is the diameter of the strands in the meshwork.

Open area ratio (R): the ratio of the open area of a net to the area of its mouth; R is given by the equation:

$$R = \frac{a \cdot \beta}{A}$$

where a is the porous area of the net.

Clogging: the process by which the porosity and filtering area ratio of a net are progressively reduced by particles which adhere to the strands of gauze during filtration.

Mesh velocity (v'): the mean velocity at which the water discharges through the meshes of a plankton net; v' may be calculated from the equation:

$$v = \frac{A \cdot F \cdot V}{a \cdot \beta} = \frac{V'}{R}.$$

Approach velocity (v): the effective velocity at which the water approaches the immediate environs of the filtering surface before its acceleration through the meshes; v is given by the equation:

$$v = v' \cdot \beta .$$

Filtration pressure (ΔP): the pressure of the water flowing through a plankton net upon its filtering surface; P may be calculated from the equation:

$$\Delta P = K \cdot \tfrac{1}{2} \varrho v^2$$

where K is the *resistance coefficient* (pressure drop coefficient) of the gauze.

Drag (D) is the total resistance to the free passage of the sampler through the water; D is given by the equation:

$$D = C_D \cdot \tfrac{1}{2} \varrho V^2 \cdot A$$

where C_D is the *drag coefficient* of the sampler.

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Tests on the Accuracy of Ageing Chinook Salmon (*Oncorhynchus tshawytscha*) from their Scales[1]

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ABSTRACT

The accuracy with which several readers determined the ages of adult chinook salmon from their scales averaged 75% in a test that used scales from fish of known ages. Their consistency in assigning the same age to a scale when presented with the same selection of scales on two occasions averaged 76%. In these tests the readers derived age composition arrays which were similar to the true age compositions of the two samples. When several pairs of readers assigned ages to a large numbers of scales from fish of unknown ages agreement within pairs was good (roughly 75%), and among the pairs the derived age compositions were very similar. The levels of both accuracy and consistency achieved in these tests indicate that experienced personnel, using good scale-reading equipment, are able to produce age composition data that could be used as reliable parameters in chinook salmon population analyses.

INTRODUCTION

Salmon scale "readers" appear to be in general agreement that chinook salmon scales are particularly difficult to age with confidence. The difficulty arises from the complexity of the chinook salmon's life history, and because the life history of the species can vary considerably among stocks and races, and even among individuals of the same race.[2]

Young chinook salmon may migrate from fresh water to the ocean within hours of emergence, or after periods of residence that can vary from days, weeks, or months to as much as several years. They may remain at sea for

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[2] In this context a "stock" of salmon has the general meaning that they belong to a particular river system, including its tributaries (for example, the Fraser River stocks of chinook salmon, which are composed of a number of races). Using Mason's (1965) definition, a "race" is considered to be "a population of chinook salmon which spawns in a particular river or tributary at a particular time of the year."

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several months to as long as 6 or more years. Some young leave the stream at the very beginning of scale formation, whereas others migrate with the body fully covered with scales, and with scales that already show numbers of freshwater circuli.

Differences among young fish also occur, depending upon where and for how long they sojourn before they finally enter the ocean proper. Apparently there is much variation in the time they spend in or near river mouths or in estuaries. The wide range of physical and biological differences in both their freshwater and marine habitats is reflected in comparable variation in their growth and, in turn, therefore, in their scale patterns. To the scale reader the end result of all this variability in the life history of the chinook salmon, particularly during the early period, is that its scales are difficult to interpret for age because he frequently lacks the criteria upon which such an interpretation can be based with confidence.

In the current program to evaluate the efficiencies of chinook salmon hatcheries on the Columbia River,[3] the age compositions of the catches and escapements of chinook salmon are needed in computing the contributions of the hatcheries to the fisheries, and in computing the survival of different broods at different ages. Therefore, because it was recognized that there was a problem in the ageing of chinook salmon from their scales, tests were conducted to determine how well or how poorly chinook salmon scales could be read. The purpose of this document is to report the results of these tests.

METHODS

Three tests were made, each involving experienced scale readers from one Canadian and several United States fisheries agencies. In this report the scale readers and the agencies to which they belong are not identified; instead a letter serves to designate each individual reader.

In the first test 200 scales of known age were used. The ages were known because the scales came from recaptured hatchery fish that had been marked by a double finclip when liberated. Sets of impressions were made of these scales and sent to the different readers. No information, other than that they were chinook salmon scales, was provided to the readers. In some cases the readers were not aware that they were engaged in a test, or that the true ages of the scales they were examining were known. Those who selected the scales were not otherwise involved in the test. In addition, the selectors chose for the test only scales which they themselves considered readable.

Several months later impressions of these same scales, arranged in different order, were again sent to the readers. All other conditions of this second part of this test were the same as for the first. Thus, in the first test it was possible to determine each reader's accuracy in assigning an age to a scale, and also the consistency with which he assigned a particular age to each scale in the two readings.

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[3] The main objective of this program is the assessment of the efficiency of several hatcheries in their production of autumn ("fall") runs of chinook salmon. This is being done by determining the catches (both sport and commercial from California to southeast Alaska) and escapements resulting from the releases of the progeny from four brood stocks (1961–64).

In the second test the same 200 scales plus 200 similarly selected scales of known age were sent to the readers. However, on this occasion, for each of the 400 scales the fork length of the recaptured fish, and the month and location of its capture were provided. The main objective of this second test was to assess to what extent, if any, the readers were able to improve their age determinations by making use of the additional information. All other conditions of this test were the same as for the first.

In the third test scales of unknown age, taken from troll catches off the west coast of Vancouver Island, were used. The main objective of this test was to compare the age determinations made by different pairs of readers. As is commonly known, the west coast of Vancouver Island troll fishery exploits a mixture of stocks from many river systems and from United States hatcheries.

The equipment used by the different readers varied among the agencies (Appendix), but it was that which they preferred and with which they were most familiar.

The complete data produced by these tests are on file at the Fisheries Research Board of Canada, Biological Station, Nanaimo, B.C.

RESULTS

TEST 1. SCALES OF FISH OF KNOWN AGE

SCALES 1–200, READ TWICE

With each of the four readers, and in both readings of the first 200 scales, the errors in assigned ages included several age-classes and were sometimes high relative to the correct number of scales belonging to a particular age-class (Table I). However, among the 1600 determinations the total number of wrong age assignments was only 403, or 25.2%. In the first reading the correct assignments by the four readers averaged 76.0, 64.0, 69.5, and 83.0% of the 200 scales, and in the second reading, 82.5, 60.0, 77.0, and 86.5% (Table II). For the four readers and the two readings combined, the overall average was 74.8% correctly assigned.

The rates of consistency with which the four readers assigned a particular age (correctly or incorrectly) to each scale in the second reading were 79.5, 69.0, 72.0, and 83.5% (Table III). The average for the four readers amounted to 76.0% — that is, among them they gave the same age assignments to 608 out of 800 determinations at the second reading as they had done at the first. All four readers achieved a high rate of consistency with scales which they considered to be of age 0.2 (range, 76.1–95.6%).

As might be expected, the readers' consistency in general paralleled their accuracy. The two more important exceptions to this were with scales which were read (correctly or incorrectly) as 0.1's and 0.2's. As the following tabulation indicates, which is based on all the readings, the readers tended

TABLE I. The ages assigned to the first 200 scales, by four readers for each of the two readings separately and for both readings combined, as percentages of the number of scales of each true age-class.[a]

True age	No. of scales	First reading										Second reading									1st and 2nd readings combined									
		0.1	0.2	1.1	0.3	1.2	0.4	1.3	2.2	1.0	NR[b]	0.1	0.2	1.1	0.3	1.2	0.4	1.3	2.2	NR	0.1	0.2	1.1	0.3	1.2	0.4	1.3	2.2	1.0	NR
Reader A																														
0.1	31	45.2	41.9	6.5							6.5	64.5	29.0	6.5							54.8	35.5	6.5							3.2
0.2	115		80.9		12.2	6.1					0.9		89.6		3.5	6.1				0.9		85.2		7.8	6.1					0.9
1.1	2		50.0	50.0									50.0	50.0								50.0	50.0							
0.3	38				86.8	2.6		2.6			7.9		5.3		89.5					5.3		2.6		88.2	1.3		1.3			6.6
1.2	10				20.0	70.0					10.0		10.0		30.0	50.0				10.0		5.0		25.0	60.0					10.0
1.3	4							100.0								50.0		50.0							25.0		75.0			
Reader B																														
0.1	31	74.2	25.8									54.8	35.5	3.2		3.2	3.2				64.5	30.6	1.6		1.6	1.6				
0.2	115	3.5	65.2		28.7	1.7		0.9					64.3	0.9	31.3	1.7	1.7				1.7	64.8	0.4	30.0	1.7	0.9	0.4			
1.1	2		50.0	50.0										50.0	50.0							50.0	50.0							
0.3	38		7.9	2.6	55.3	31.6	2.6						5.3		50.0	36.8	2.6		5.3			6.6	1.3	52.6	34.2	2.6		2.6		
1.2	10		10.0		30.0	50.0		10.0							40.0	50.0	10.0					5.0		35.0	50.0	5.0	5.0			
1.3	4					25.0		75.0										100.0							12.5		87.5			
Reader C																														
0.1	31	74.2	6.5	12.9						6.5		80.6	6.5	12.9							77.4	6.5	12.9						3.2	
0.2	115	2.6	80.9		12.2	4.3						2.6	80.0	0.9	14.8	1.7					2.6	80.4	0.4	13.5	3.0					
1.1	2			50.0	50.0									50.0	50.0								50.0	50.0						
0.3	38		28.9	5.3	39.5	15.8	2.6	2.6	5.3				10.5	2.6	73.7	13.2						19.7	3.9	56.6	14.5	1.3	1.3	2.6		
1.2	10		10.0		20.0	50.0		20.0					30.0		20.0	40.0			10.0			20.0		20.0	45.0		10.0		5.0	
1.3	4					50.0		50.0										100.0							25.0		75.0			
Reader D																														
0.1	31	61.3	22.6	12.9	3.2							61.3	29.0	9.7							61.3	25.8	11.3	1.6						
0.2	115	1.7	89.6		7.0	1.7							97.4		2.6						0.9	93.5		4.8	0.9					
1.1	2		50.0	50.0									50.0	50.0								50.0	50.0							
0.3	38		5.3		84.2	10.5							5.3	2.6	78.9	13.2						5.3	1.3	81.6	11.8					
1.2	10		10.0	10.0	10.2	70.0							20.0		10.0	70.0						15.0	5.0	10.0	70.0					
1.3	4							100.0										100.0									100.0			

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[a] In this report ages are designated according to the European system. Thus, a 0.1 fish has no freshwater annulus, but has one ocean annulus; it is therefore in its 2nd year of life, having gone to sea in its 1st. A 1.2 fish has one freshwater annulus and two ocean annuli; it is therefore in its 4th year of life, having gone to sea in its 2nd. According to the Gilbert and Rich (1927) system, the fish in these two examples would have had ages designated as 2_1 and 4_2 respectively.

[b] Not read.

to be more consistent in reading scales as 0.1's and 0.2's than they were accurate in assigning ages to 0.1 and 0.2 scales:

True age:	0.1	0.2	1.1	0.3	1.2	1.3
No. of readings	248	920	16	304	80	32
% accuracy	62.2	81.1	50.0	69.2	58.6	82.1
% consistency	72.8	87.1	55.6	63.8	61.0	61.1

TABLE II. Percentages of correct assignments for each age-class in two readings of first 200 scales by four readers.

True age	No. of scales	Reader								
		A	A	B	B	C	C	D	D	Avg
0.1	31	45.2	64.5	74.2	54.8	74.2	80.6	61.3	61.3	64.5
0.2	115	80.9	89.6	65.2	64.3	80.9	80.0	89.6	97.4	81.0
1.1	2	50.0	50.0	50.0	50.0	50.0	50.0	50.0	50.0	50.0
0.3	38	86.8	89.5	55.3	50.0	39.5	73.7	84.2	78.9	69.7
1.2	10	70.0	50.0	50.0	50.0	50.0	40.0	70.0	70.0	56.3
1.3	4	100.0	50.0	75.0	100.0	50.0	100.0	100.0	100.0	84.4
Total or avg	200	76.0	82.5	64.0	60.0	69.5	77.0	83.0	86.5	74.8

TABLE III. The consistency with which the four readers assigned the same age to a scale in the second reading of the first 200 scales as they did in the first.[a]

Ages assigned	Consistency		Ages assigned	Consistency	
	No.	%		No.	%
	Reader A			***Reader B***	
0.1	13/15	86.7	0.1	17/27	63.0
0.2	98/109	89.9	0.2	67/88	76.1
1.1	3/3	100.0	1.1	1/2	50.0
0.3	34/51	66.7	0.3	37/57	64.9
1.2	9/7	52.9	1.2	12/20	60.0
1.3	2/5	40.0	0.4	1/1	100.0
Total	159/200	79.5	0.3	3/5	60.0
			Total	138/200	69.0
	Reader C			***Reader D***	
0.1	22/28	78.6	0.1	15/22	68.2
0.2	85/101	84.2	0.2	108/113	95.6
1.1	4/7	57.1	1.1	2/6	33.3
0.3	24/48	50.0	0.3	30/42	71.4
1.2	7/11	63.6	1.2	8/13	61.5
1.3	2/4	50.0	1.3	4/4	100.0
NR	0/1	0.0	Total	167/200	83.5
Total	144/200	72.0			

[a] Whether or not a reader made a correct or an incorrect age assignment at either reading is, of course, ignored in this comparison.

Among the 403 instances of misageing, 44 (10.9%) were due to underageing by 1 ocean year, but with the correct freshwater age; 200 (49.6%) were due to over-ageing by 1 or more ocean years, but with the correct freshwater age; and 107 (26.6%) were due to assigning 1 freshwater year to scales that had none (however, of these, 51, or 12.7% of the 403 misaged scales, had been given the correct total age). Of the remaining 52 (12.9%) scales, 12 (3.0%) were not assigned ages; 23 (5.7%) had the correct total age, but both the freshwater and ocean ages wrong; and 17 (4.2%) had other errors. Of the 1588 scales that were read, 1271 (80.0%) had been given the correct total age; 1381 (87.0%) had been given the correct freshwater age; and 1255 (79.0%) had been given the correct ocean age.

TEST 2. SCALES OF FISH OF KNOWN AGE

SCALES 1–400, READ WITH INFORMATION ON CAPTURE OF FISH

In general, little improvement resulted from readers being supplied with information for each scale on the fork length of the fish, and the month and place of its capture (Table IV). The principal exception to this was with the

TABLE IV. The percentages of correct age assignments which readers achieved in tests 1 and 2.[a]

Reader	1	2	3	4	1	2	3	4	1	2	3	4
	Age 0.1				*Age 0.2*				*Age 1.1*			
A	45.2	64.5	67.7	82.0	80.9	89.6	87.0	68.0	50.0	50.0	50.0	–
B	74.2	54.8	90.3	92.0	65.2	64.3	69.6	68.0	50.0	50.0	50.0	–
C	74.2	80.6	83.9	90.0	80.9	80.0	93.0	68.0	50.0	50.0	50.0	–
D1	61.3	61.3	83.9	94.0	89.6	97.4	87.8	68.0	50.0	50.0	50.0	–
D2	–	–	83.9	92.0	–	–	97.4	88.0	–	–	50.0	–
	Age 0.3				*Age 1.2*				*Age 0.4*			
A	86.8	89.5	94.7	70.0	70.0	50.0	40.0	–	–	–	–	62.0
B	55.3	50.0	89.5	78.0	50.0	50.0	60.0	–	–	–	–	76.0
C	39.5	73.7	73.7	48.0	50.0	40.0	40.0	–	–	–	–	40.0
D1	84.2	78.9	86.8	82.0	70.0	70.0	60.0	–	–	–	–	88.0
D2	–	–	92.1	90.0	–	–	30.0	–	–	–	–	86.0
	Age 1.3				*All ages*							
A	100.0	50.0	75.0	–	76.0	82.5	82.5	70.5				
B	75.0	100.0	100.0	–	64.0	60.0	76.5	78.5				
C	50.0	100.0	100.0	–	69.5	77.0	85.0	61.5				
D1	100.0	100.0	100.0	–	83.0	86.5	85.5	83.0				
D2	–	–	–	–	–	–	90.5	89.0				

[a] Column 1 — first reading of first 200 scales, read with no accompanying information; column 2 — second reading of first 200 scales, read with no accompanying information; column 3 — third reading of first 200 scales, read with information on fork length and month and place of capture; column 4 — only reading of second 200 scales, read with information on fork length and month and place of capture. (Readers D1 and D2 were attached to the same fisheries agency.)

0.1 fish. With this age-class the third reading of the first 200 scales, and the single reading of the second 200 scales, provided rates of correct age assignment by all readers that were appreciably higher than those achieved when the scales were read without the additional information.

TRUE AND ASSIGNED AGE COMPOSITIONS

The two tests provided 18 separate age composition arrays which can be compared with the true age compositions of the two samples. Regardless of the errors that they made (as has been described in the foregoing text), most of the readers derived age compositions which were fairly similar to the true ones (Table V). The most prominent exception to this was with the single reading of the second lot of 200 scales (despite the fact that these scales were accompanied with information on length and time and place of capture), when the five readers together named six age-classes which were not actually present in the sample.

Three factors were probably mainly responsible for the degree of accuracy which the readers attained in determining the age compositions of the two samples: (*a*) in most instances the readers correctly interpreted in terms of freshwater and ocean ages what they identified on the scales as circuli and annuli; (*b*) all the readers had some general knowledge of the life history of chinook salmon, and specifically of the ages at which they commonly spawn or are taken in the fisheries, and this knowledge no doubt influenced to some degree their interpretations of the markings on the scales which they observed; (*c*) in each test the readers made errors of both over-ageing and under-ageing, which, by offsetting each other, promoted a more correct derivation of the *age composition* than would have been the case had their errors been in one direction only.

TEST 3. SCALES OF FISH OF UNKNOWN AGE

The main objective of this test was to compare the age assignments made by all of the readers by pairs. Five of the readers attempted to age all of the 928 scales, one reader examined 500 scales, and the seventh examined 300.

With scales which both of a pair of readers aged, the overall rate of agreement between the two readers averaged 76.6%, and ranged from 66.6 to 86.9% among the 20 different pairs (Table VI). Also, *on the average*, the pairs of readers considered 25.4% of the scales to be not readable, the range between pairs being 9.3–28.1%. The *average* number of scales which one of a pair aged but not the other amounted to only 5.4% (range, 3.2–12.0%).

All the readers found seven different age-classes, and no more, among the scales which they were able to age (Table VII).

The accuracy of the readers' age assignments cannot, of course, be assessed, since the true ages of these fish were not known. However, agreement among readers, which would indicate the level of confidence that might be attached to their results, can be examined by comparing the age compositions

Table V. The age compositions (percentages) derived by each reader compared with the true age compositions.[a]

	Age								
Reader	0.1	0.2	1.1	0.3	1.2	1.3	1.0	0.4	2.2
First reading of first 200 scales read without additional information									
A	7.3	55.4	1.6	25.4	7.8	2.6	–	–	–
B	13.5	44.0	1.0	28.5	10.0	2.5	–	0.5	–
C	13.0	53.5	3.5	16.0	9.0	2.5	1.0	0.5	1.0
D	10.5	57.0	3.0	21.0	6.5	2.0	–	–	–
True age	15.5	57.5	1.0	19.0	5.0	2.0	–	–	–
Second reading of first 200 scales read without additional information									
A	10.2	59.2	1.5	20.9	1.7	1.0	–	–	–
B	8.5	43.5	1.5	30.0	11.0	2.0	–	2.5	1.0
C	14.1	50.8	3.5	24.1	5.5	2.0	–	–	–
D	9.5	63.0	2.5	17.0	6.0	2.0	–	–	–
True age	15.5	57.5	1.0	19.0	5.0	2.0	–	–	–
Third reading of first 200 scales read with information on fork length, month, and place of capture									
A	10.8	57.2	1.5	22.7	6.2	1.5	–	–	–
B	14.0	41.0	1.0	35.0	6.0	3.0	–	–	–
C	13.0	56.0	2.5	16.5	7.0	3.5	0.5	–	1.0
D1	13.0	53.5	1.5	24.5	5.0	2.0	–	0.5	–
D2	13.5	61.5	1.0	20.5	1.5	2.0	–	–	–
True age	15.5	57.5	1.0	19.0	5.0	2.0	–	–	–

Single reading of second 200 scales read with information on fork length, month, and place of capture

	Age									
	0.1	0.2	0.3	0.4	1.1	1.2	2.1	1.3	0.5	1.4
A	24.4	20.9	26.2	19.2	–	4.1	–	2.9	0.6	1.7
B	23.5	18.0	29.0	20.5	1.0	–	–	3.0	–	5.0
C	23.1	18.1	18.1	12.6	1.5	2.5	1.0	8.5	0.5	14.1
D1	24.0	19.0	27.5	23.5	0.5	1.5	–	2.5	–	1.5
D2	24.2	24.7	26.3	22.2	0.5	–	–	0.5	–	1.5
True age	25.0	25.0	25.0	25.0	–	–	–	–	–	–

[a] In computing a reader's age composition any scales which he did not read were not included.

TABLE VI. Comparisons between pairs of readers who read chinook salmon scales of unknown age from the west coast of Vancouver Island. Five readers read all 928 scales; a sixth, 500; and a seventh, 300.

Pair	Scales aged by both readers Agreement (%)	Scales not aged by either reader (%)	Scales not aged by one reader (%)
	All (928) scales		
1×2	78.6	28.1	4.0
1×3	82.4	27.8	5.0
1×4	66.7	27.2	4.8
1×5	74.6	26.5	5.5
2×3	81.1	26.5	5.2
2×4	75.4	26.7	4.2
2×5	74.1	26.2	4.7
3×4	74.1	26.7	4.2
3×5	79.8	25.4	5.6
4×5	66.6	25.9	3.9
	500 scales		
1×6	79.6	25.0	7.4
2×6	78.4	25.8	4.6
3×6	84.5	24.0	7.6
4×6	73.1	24.8	4.6
5×6	80.8	25.8	3.2
	300 scales		
1×7	80.3	20.3	12.0
2×7	79.5	9.3	9.3
3×7	84.3	19.3	8.3
4×7	68.5	19.7	7.3
5×7	86.9	19.0	10.0
Total or avg	76.6	25.4	5.4

derived by the various pairs, using only those scales to which each member of a pair gave the same ages (both fresh water and ocean). This has been done in Table VII for the five readers who attempted to read all of the 928 scales.

In terms of the derived age compositions of the sample the agreement between the 10 pairs of readers was very good. The greatest difference among the 10 pairs of readers was with the 0.2 age-class — thus, pair 2 × 4 read 53.6% of the sample as 0.2 fish as compared with 64.8% by pair 2 × 5, a range of 11.2%. The smallest difference between the pairs was with the 0.1 age-class — thus, three pairs of readers read 3.2% of the sample as 0.1 fish as compared with 4.0% by pair 1 × 4 (a difference of 0.8%).

DISCUSSION

From the tests that made use of scales of known age it may be concluded that: (*a*) the degree of accuracy achieved in reading all the scales varied among the readers, but the overall average of approximately 75% can be considered

TABLE VII. The age compositions (percentages) derived by pairs of readers, using only those scales on whose ages they agreed. Test 3; 928 scales of unknown age.[a]

Readers	0.1	0.2	1.1	0.3	1.2	0.4	1.3
1×2	3.2	59.2	1.2	24.0	8.5	1.2	2.6
1×3	3.3	60.9	1.2	22.6	8.6	0.6	2.9
1×4	4.0	56.3	1.4	27.6	6.9	1.2	2.6
1×5	3.2	64.3	1.1	23.4	5.7	0.6	1.7
2×3	3.3	60.9	1.2	24.5	7.2	0.8	2.1
2×4	3.3	53.6	1.7	30.8	5.2	2.5	2.9
2×5	3.2	64.8	0.8	25.3	4.0	0.6	1.3
3×4	3.6	56.8	1.7	27.2	7.4	0.8	2.5
3×5	3.3	64.6	0.8	24.5	5.1	0.6	1.2
4×5	3.7	60.1	1.4	28.8	4.4	0.7	0.9
Range	0.8	11.2	0.9	8.2	4.6	1.9	2.0

[a]Each pair of readers agreed upon approximately 75% of the scales which they examined.

adequate; (*b*) the degree of accuracy differed with the true age-class, and scales with both freshwater and ocean annuli were misaged more frequently than those with only saltwater annuli; (*c*) information on length of fish and time and place of capture was of some value in improving the interpretation of the 0.1 fish, but was not especially beneficial otherwise; there is no reason to think that such information would be particularly useful in determining the ages of fish in samples comprising mixed stocks and races (except, possibly, in the case of the 0.1 fish, whose small size would likely prompt caution in assigning older ages); (*d*) the degree of consistency in reading these scales was relatively high, averaging 76% among four readers; (*e*) the age compositions of the two samples derived by the several readers were very similar, and approximated the true age compositions. To some extent this resulted from balancing-out over-ageing by under-ageing, but it was mainly due to the accuracy with which readers assigned ages to scales.

In the test which used the large number of scales from fish of unknown age, taken from catches of mixed populations, the levels of agreement within pairs of readers in assigning ages to scales were high. Also, the age composition arrays derived from these scales by 10 pairs of readers were very similar.

Thus, it is the writers' opinion that experienced salmon scale readers, using good equipment, can derive chinook salmon age composition data that are sufficiently accurate as to make them useful parameters for salmon population analyses.

A further point might be discussed. Does the accuracy achieved in assigning ages to chinook salmon scales differ significantly from that achieved with the scales of other Pacific salmon? At this time we have only certain sockeye salmon data that might be compared. Actual *accuracy* cannot be compared because the true ages of these fish were not known. However, Table VIII

TABLE VIII. The percentage agreement achieved by pairs of readers who aged sockeye salmon scales of Canadian (100 scales), Japanese (100 scales), and United States (255 scales) origin.[a]

Pairs of readers:	AB	AC	AD	AE	AF	BC	BD	BE	BF
Canadian sockeye	90.0	91.0	91.0	92.0	–	83.0	82.0	88.0	–
Japanese sockeye	45.0	76.0	75.0	75.0	67.0	46.0	47.0	46.0	44.0
U.S. sockeye	65.5	76.5	78.4	71.4	70.6	58.0	56.5	53.7	50.2

Pairs of readers:	CD	CE	CF	DE	DF	EF
Canadian sockeye	100.0	85.0	–	86.0	–	–
Japanese sockeye	87.0	83.0	75.0	85.0	81.0	78.0
U.S. sockeye	82.4	78.0	77.7	75.7	75.3	87.1

[a] Data from Anon. (1956). The Japanese sockeye were taken on the high seas, so that their actual origin is not known; it could have been either Asian or North American, or both.

shows the *degree of agreement* reached between pairs of readers who determined the ages of sockeye salmon scales obtained from Japanese, United States, and Canadian sources (Anon., MS, 1956).[4] The comparison makes it very apparent that there were many cases of disagreement. (The scales included freshwater ages of from 1 to 4 years, and total ages of from 2 to 7 years; the consistent high rate of agreement achieved with the Canadian scales was no doubt due to the fact that among them there were fewer age-classes (both ocean and freshwater) than there were among the Japanese and United States scales.)

In this report no material is presented that describes the different kinds of scales used in the tests, nor is an attempt made to indicate the specific characteristics of scales upon whose interpretation the readers either agreed or disagreed. Probably, there will always be considerable disagreement in the interpretation of individual chinook salmon scales, even among experienced scale readers. The reasons for this, as has been mentioned, arise from the complexity and variability in the life history of the chinook salmon. However, the results of the tests do suggest that improvement in accuracy and/or consistency might be achieved in several ways. In the first place, it is considered that to attain high levels of *consistency* in assigning ages, good, modern equipment must be used (see Appendix), and the readers should be trained and experienced. Secondly, the fund of reliable criteria that could be used in making interpretations of scale patterns must be increased, if improvements in either accuracy or consistency are to be made. This could be achieved if information gained from examining chinook salmon scales from many sources, of fish which have experienced a wide variety of environments, could be disseminated more widely. Finally, the results of the tests suggest that useful criteria for interpreting scales probably also would be gained if readers could compare the processes by which they gave age assignments to individual scales, particularly those scales on whose ages they disagreed.

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[4] See footnote to Table VIII.

ACKNOWLEDGMENTS

The writers are most appreciative of the work of the following who read the scales used in these tests:

Messrs E. E. Weiss, Howard Jensen, and Mel Woodall of the Fish Commission of Oregon; Mr K. H. Mosher of the U.S. Bureau of Commercial Fisheries, Seattle, Wash.; Miss Ruth R. Mandapat of the Washington State Department of Fisheries; Mr D. W. Jenkinson, Mr E. A. R. Ball, and Mrs Sigrid Ludwig of the FRBC, Biological Station, Nanaimo, B.C.

Mr Earl Pulford of the Oregon Fish Commission is especially thanked for selecting the scales that were used in the first two tests. Constructive comments on this paper were made by Messrs K. H. Mosher, F. H. Summer, R. Major, P. D. Zimmer, and L. H. LeMier.

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APPENDIX — EQUIPMENT USED

The following apparatus was used by the several agencies participating in these tests:

OREGON FISH COMMISSION (REGIONAL OFFICE, CORVALLIS)
Eberbach Projector, Cat. No. 72–402, with 24-inch screen and 80× magnification.

OREGON FISH COMMISSION (RESEARCH HEADQUARTERS, CLACKAMAS)
Bausch & Lomb Tri-Simplex micro-projector, vertical (downward) projection, 21–23× magnification (occasionally, 42–46× for more detailed study).

WASHINGTON STATE DEPARTMENT OF FISHERIES (OLYMPIA)
Monocular microscope mounted on a Spencer Ortho-Illuminator; Model 600; with prism and mirror for reflection to table. Magnification from 6 to 90×. Detailed description given by R. R. Mandapat, Washington Department of Fisheries, in "Age analysis technique, utilizing fish scales, presently used by the Washington Department of Fisheries." Manuscript, 1968.

UNITED STATES BUREAU OF COMMERCIAL FISHERIES, SEATTLE, WASHINGTON
Microscope with a 90° prism and plate glass mirror for projection onto white celluloid sheet. Magnifications of 40 and 82.5× used. Detailed description given by K. H. Mosher in U.S. Fish and Wildlife Service Bull. No. 54, Vol. 51, 1950.

FISHERIES RESEARCH BOARD OF CANADA (BIOLOGICAL STATION, NANAIMO, B.C.)
Leitz Prado No. 500 micro-projector, Cat. No. 34010A; vertical projection by means of ocular prism and mirror; 100× magnification.

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pp. 77–82

Trends in the Marine Fisheries of the Continental Shelf of the Eastern United States

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Woods Hole, Massachusetts

The Continental Shelf of the eastern United States, including that of the Gulf of Mexico, is a rich area containing a great array of valuable species of fish and shellfish which have been harvested in quantity for many years (Figure 1). The landings from this coastal area, which extends from the Canadian border in the northeast to the Mexican border in the southwest, have shown a general trend upward during the last 35 years increasing from 600,000 metric tons in the early 1930's to almost 2,000,000 metric tons in 1962 (Figure 2). This represents an average increase of about 13% per year. In the early part of this period the landings doubled in 14 years and in the latter part (up to 1962) they doubled again in 15 years.

If we were to extrapolate the recent 35 year trend we would forecast another doubling of the catch by 1980 with landings nearing 4,000,000 metric tons. However, such an increase is not likely to occur. The long upward trend in total landings has been maintained by shifting effort to previously unexploited or underexploited species or stocks. It is highly unlikely that sufficient other unexploited stocks exist to support the present increasing trend much longer if at all.

Extreme changes in the species compositions of the total landings from the area have taken place since 1930. In that year haddock accounted for almost 17% of the total landings while in 1956 haddock landings accounted for only 4% of the total. In 1956 menhaden landings represented 60% of the total, but by 1966 had dropped to well below one half that of peak years and accounted for only 22% of the total landings from the area. Total landings of all species were maintained by increased landings of such other species as silver hake, herring, and haddock.

The changing species composition of the total landings is shown by the catch statistics of the more important species or species groups over the period 1930 to 1966. These are presented graphically in Figures 3 to 15. These graphs present a variety of patterns. Changes in landings are the result of two factors: changes in abundance or availability, and changes in market demand. Among the various fisheries on the eastern shelf and Gulf of Mexico there are examples of the interaction of these two forces in all their possible combinations.

The history of the Georges Bank haddock fishery is one of the most interesting (Figure 3). This fishery was carried out almost exclusively by the United States until 1962. In 1930, during its initial exploitation phase, landings amounted to over 100,000 metric tons. Subsequent to this and for about 25 years the landings fluctuated around 50,000 metric tons. During this time there were changes in abundance but the relative stability in landings was probably the result of economic factors in the United States fishery. Canada entered this fishery in 1962 and the Soviets began reporting an incidental catch of haddock from Georges Bank about the same time. As a result of this foreign effort, total haddock landings by 1964 were above the long term average of United States landings. In 1965 there was a sudden and dramatic increase to over 150,000 metric tons, the highest on record. This was the result of increased abundance and increased effort. An unusually large year class entered the fishery in that year providing an unusual abundance of small fish. The Canadians increased their catch to 15,000 metric tons while the Soviets took 82,000 metric tons, all this in the last six months of the year. In 1966 Georges Bank haddock were still very abundant and the landings high, although lower than in 1965. It is interesting to note that United States landings held steady during these two years of high abundance while foreign fleets were reaping a large harvest. The United States took less than half the crop. Apparently economic factors in the United States fishery determined the level of United States landings in 1965 and 1966 rather than abundance of fish.

The future of the Georges Bank haddock fishery is uncertain. There has not been a good year class since 1963 and landings will inevitably decline in the immediate future. For the long term we can expect changes in landings to reflect changes in abundance. Since a large mobile fleet of vessels is available to take advantage of sudden increases in availability of fish we can expect the kind of pulse fishing that occurred in 1965 to be repeated when and if future bursts of abundance occur, unless this kind of exploitation is prevented by international agreement.

The redfish fishery in the Gulf of Maine had an interesting rise and fall (Figure 4). A market for this fish under the name of "Ocean Perch" was developed in the 1930's. The fish was abundant

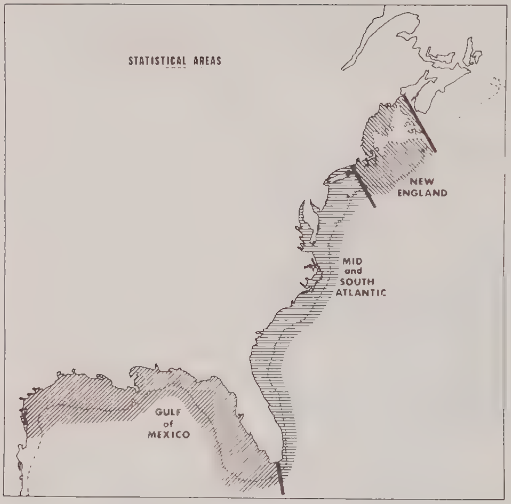

FIGURE 1.—Statistical areas used in this report.

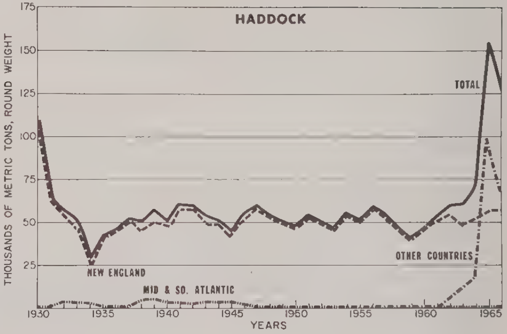

FIGURE 3.—Haddock landings. For explanation see Figures 1 and 2.

from the Gulf of Maine northward to Labrador and Greenland. The stocks closest to home were quickly exploited with landings reaching 60,000 metric tons for the Gulf of Maine in 1941. Abundance of this slow growing fish soon declined and the decrease in landings for the Gulf of Maine from 1941 to 1954 reflects this decline in abundance. The market for redfish in the United States in recent years has softened and the decrease in landings in the 1960's is the result of lower demand. Actually, abundance in the Gulf of Maine as represented by catch per day has been increasing since 1960 but the landings are still declining. The future of this fishery depends upon consumer demands.

The Silver Hake fishery offers a good example of the effects of market demand (Figure 5). Silver hake is the most abundant groundfish on the New England banks but the United States market can absorb only a small part of the potential harvest. United States landings increased steadily for 20 years reaching a high of a little over 50,000 metric tons in 1957. Since then United States landings have generally decreased. The Soviet Union turned its attention to this species in 1963. When the Soviet consumer found this a very acceptable fish, the Soviet fleet concentrated on it and, in 1965 landed almost 300,000 metric tons. In 1966 the Soviet catch dropped drastically due to a decrease in availability. It is not yet clear whether this decreased availability represents a decrease in abundance. In any case, the spurt in landings since 1962 is the result of increased demand, in this case from a European country.

Landings of cod from New England banks by United States fishermen declined from 1930 to 1953 as the market for this species declined (Figure 6). Since that year United States landings have stabilized. Cod landings in the United States are, for the most part, an incidental catch in the haddock fishery. During the last few years other countries have directed their attention to cod in the area and have taken cod along with haddock. Spain, USSR, and Canada are the countries concerned. This increased foreign catch has caused the total landings of cod from the area to rise to levels above that of 1930.

The flounder fishery has had its ups and downs (Figure 7). The statistics presented here represent primarily the yellowtail flounder, which is taken mostly by the New Bedford fleet. The two peaks in the land-

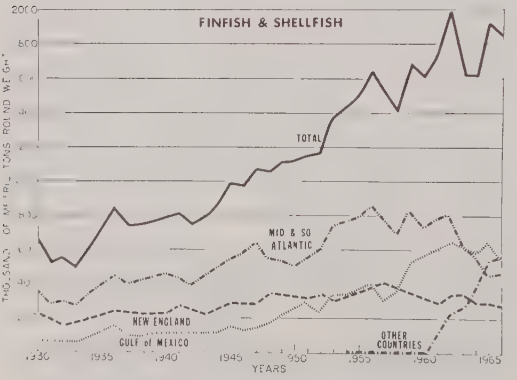

FIGURE 2.—Total landings of all species of finfish and shellfish from the continental shelf of the eastern United States including that of the Gulf of Mexico. United States landings are broken down into three areas as shown in Figure 1.

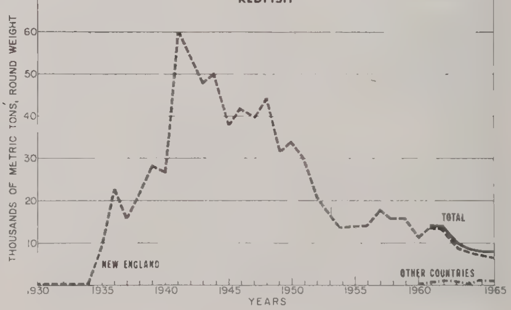

FIGURE 4.—Redfish landings. For explanation see Figures 1 and 2.

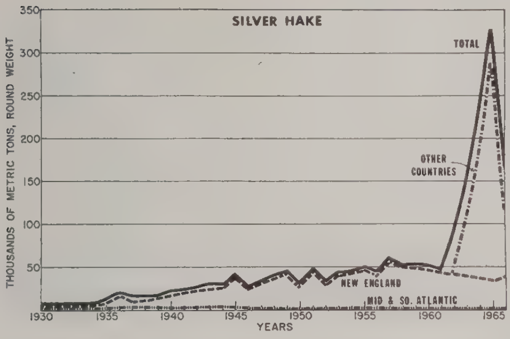

Figure 5.—Silver hake landings. For explanation see Figures 1 and 2.

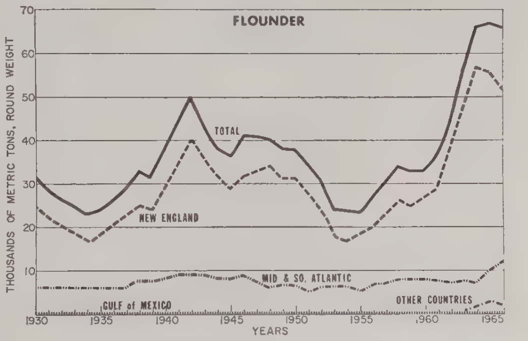

Figure 7.—Flounder landings. For explanation see Figures 1 and 2.

ings curve are the result of increased abundance. The market for this species is now strong, but landings are decreasing because of decreasing abundance. The future of this fishery no doubt, depends largely upon the vagaries of nature, since the demand will likely remain high.

The pattern of herring landings (Figure 8) is a little more complicated. The New England landings represent United States catches of inshore immature fish (Maine sardines) while the "other countries" landings are landings of mature fish by the Soviet Union from Georges Bank. The Georges Bank stock was completely unexploited until the Soviets started fishing it in 1961. The drop in the Soviet catch in 1965 was due to a reduction in the quota set by the Soviets for herring that year; which is another way of saying the market demand was less. The other year to year fluctuations in landings, in both the Soviet and the United States catches, which are rather sharp, are from changes in availability which are still unexplained.

The fishery for menhaden, a group of species used for meal and oil, has experienced a dramatic rise and fall over the years (Figure 9). The rise in this fishery was, at least in part, a response to the decline in the California sardine fishery, an industry which has never recovered. The decline in the menhaden fishery, like that of the California sardines, has occurred in the face of a good demand for the fish. The market for menhaden in the United States is firm but the fish cannot be found. It will be noted that a weakening trend in the Atlantic fishery after 1956 was offset by a rise in landings from the Gulf of Mexico but landings from this area dropped sharply in 1966 so that total landings in 1966 were less than 40% of the level reached in the peak year. Total landings of menhaden in 1967 promise to be about the same as in 1966. The drop in menhaden abundance is the result of a series of very poor year classes since 1958 coupled with very intensive exploitation of young fish. The future of this fishery is very uncertain. The causes of the fluctuations in recruitment and the importance of conditions in the estuarine nursery areas must be understood and the fishery brought under regulations based on scientific knowledge of the allowable harvest for any given recruitment. Future harvests cannot be forecast at this time.

Sea Scallops enjoy a strong market and landings generally show a rising trend with an interesting hump centered at 1961–1962 (Figure 10). This hump was due to an unusually large year class of scallop that was recruited in 1959 on Georges Bank, the most important scallop bank in the area. At that time the market was good and the United States was able to increase its take of the species. The total landings rose sharply after Canadians built a fleet of vessels to harvest this crop. As this peak of abundance passed, United States landings from Georges Bank dropped sharply. Both Canadian and

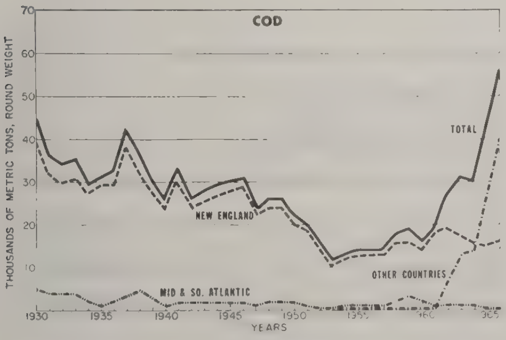

Figure 6.—Cod landings. For explanation see Figures 1 and 2.

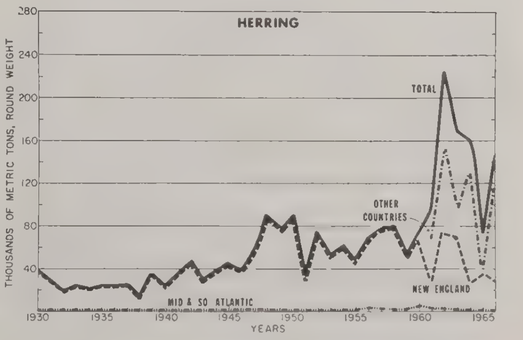

Figure 8.—Herring landings. For explanation see Figures 1 and 2.

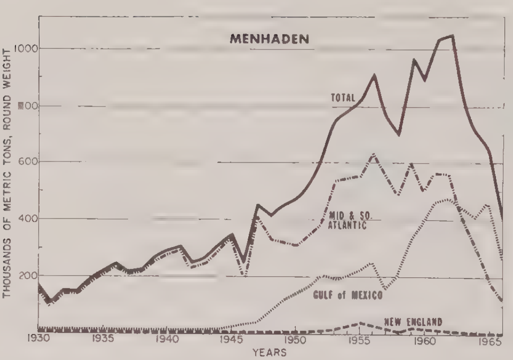

FIGURE 9.—Menhaden landings. For explanation see Figures 1 and 2.

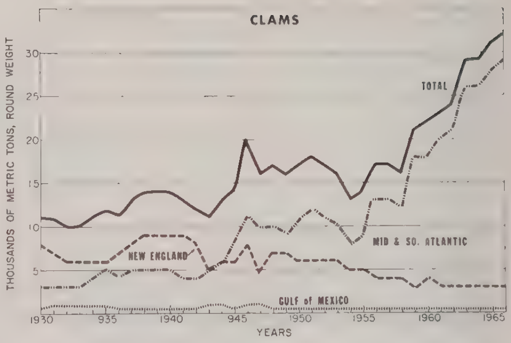

FIGURE 11.—Clam landings. For explanation see Figures 1 and 2.

United States vessels then turned to beds in the middle Atlantic Area so that total landings did not drop below the level of 1959, and in 1966 started rising again. The "middle and south Atlantic" statistics include some calico scallops, a species which is very abundant in some areas but which has not been accepted in the market until very recently. It is quite possible that scallop landings will show a sharp increase as this species gains favor in the market place. Georges Bank sea scallop landings no doubt will depend upon levels of recruitment.

The clam fishery (Figure 11) represents an interesting case of substitution of species. The New England clam fishery based on the soft shell and quahoug has suffered a slow decline due to pollution and habitat destruction. This loss has been more than compensated for by the development of the surf clam fishery in the middle Atlantic states so that since 1954 the total clam production for the eastern United States shows a sharply ascending curve. This increase can be expected to continue for some time as the known reserves are not being fully exploited.

The decline of the oyster fishery is well known to any one who can remember the days when oyster stew was a common economical household dish and to the connoisseur who now has to pay a handsome price for this delicacy on the half shell. The production of oysters today is only half that of the 1930's (Figure 12). The New England fishery that depended upon transported seed declined in the 1940's as sets failed in New York and Connecticut. Landings in the middle and south Atlantic area (primarily Chesapeake Bay) underwent a steep decline, attributed to pollution and disease, that started in 1955 and reached its lowest point in 1963. Production in the Gulf of Mexico has fluctuated irregularly, over the years.

The future of the oyster industry in the United States is uncertain. No doubt the demand for this luxury item will continue strong so that there will be ample incentive for the industry to increase its production. Solution of the mortality problems and perhaps new culture methods will be required to save this valuable fishery.

The crab fishery presents a more optimistic picture (Figure 13). The landings of this specialty item have shown a general upward trend since the early 1930's. As population and personal income increase in the United States, demand will continue to increase. Present evidence indicates that the natural supply of this species is ample to meet this demand for a few years at least.

Lobster, like the oyster, is an example of a luxury item for which the demand far exceeds the supply. However, the landings of northern lobster (New England landings in Figure 14) have held relatively steady since 1950. During this time there has been a drastic rise in price resulting in increasing pressure to increase the catch. The number of

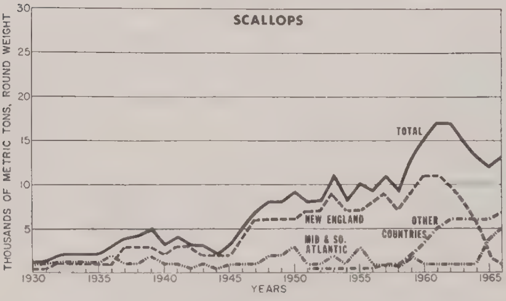

FIGURE 10.—Sea scallop landings. For explanation see Figures 1 and 2.

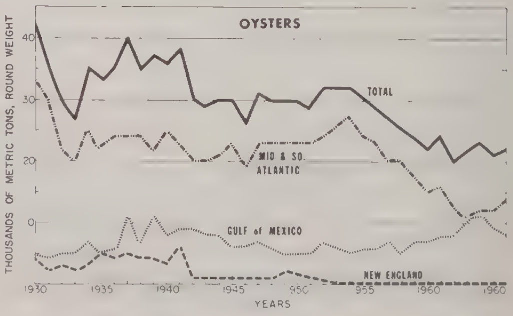

FIGURE 12.—Oyster landings. For explanation see Figures 1 and 2.

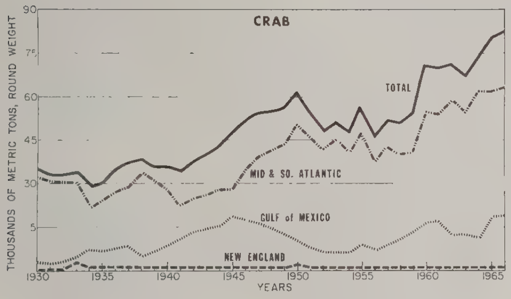

FIGURE 13.—Crab landings. For explanation see Figures 1 and 2.

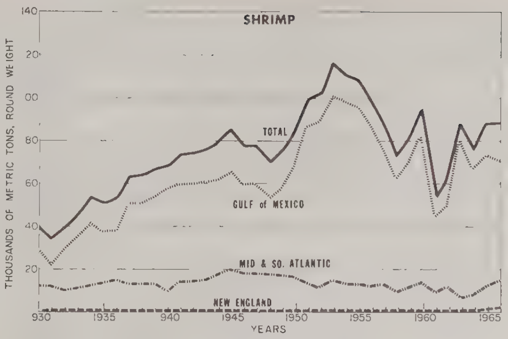

FIGURE 15.—Shrimp landings. For explanation see Figures 1 and 2.

lobster fishermen has increased as has the number of pots set but the catch holds steady. Management of this fishery is of great importance. Although there is no scientific evidence proving the effectiveness of present regulations, one wonders what the landings statistics would look like if the lobster fishery had been unregulated over the years.

What of the future of this fishery? Judging from the landings statistics one can conclude that nature is providing a rather stable supply of this delicacy and that the landings of inshore lobsters will hold steady. What happens to the price will depend upon economic conditions and peoples' determination to have a lobster dinner at any cost.

There is a deepwater offshore lobster fishery developing that may become important in the future. So far the dragger landings are a small fraction of the total but there is a reserve offshore of some magnitude. Another possibility that needs exploring is commercial lobster culture. The techniques for culture have been developed but at present the raising of lobsters for the trade is not economically feasible.

Shrimp is another delicacy that has enjoyed an increasing market in the United States. For many years this market was supplied by the white shrimp that were fished inshore by small vessels. The statistics for the Atlantic Coast (Figure 15) refer to this species. There has been some decline in this fishery since 1945 probably due partly to pollution and partly to competition from the Gulf fishery. Because the shrimp is essentially an annual, availability is notoriously variable.

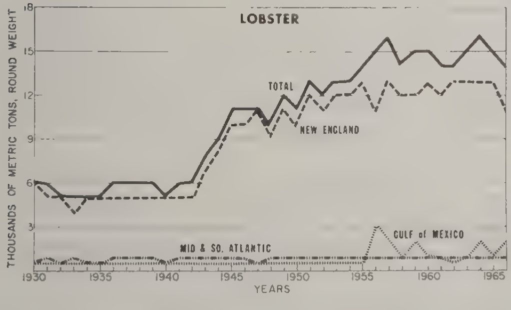

FIGURE 14.—Lobster landings. For explanation see Figures 1 and 2.

In the Gulf of Mexico the white shrimp fishery developed rapidly until 1945 and then started to decline. In the 1950's the offshore pink and brown shrimp fisheries developed as consumers began to accept these species. A rapid increase in landings resulted, reaching a peak in 1954. Since then landings have varied widely due primarily to annual changes in availability. For the past few years total landings from the entire area have averaged about 80,000 metric tons but we know at this writing that landings in 1967 will break all records and will exceed the 115,000 metric tons landed in 1953. The future of the United States coastal shrimp fishery is difficult to forecast. Certainly market demand will remain high and landings may increase but annual variations in availability will continue to cause sharp fluctuations.

In conclusion, there are a wide variety of important fisheries along the eastern Atlantic and Gulf Coasts of the United States. Some of these are inshore, are fished solely by the United States, and are under the exclusive jurisdiction of the United States. Others are carried out in international waters where the resource is, or can be, exploited by a number of nations and where management depends upon international agreements.

The most important inshore fisheries are for lobster, crab, white shrimp, clams, oysters, and menhaden. All of these except clams and crabs are now producing at or beyond their maximum sustainable levels. Fluctuations in annual landings in these species now result from fluctuations in recruitment or availability rather than from changes in demand and effort. Significant increases in total tonnage from the inshore waters will depend upon the development of new fisheries or a dramatic return of the menhaden. Extensive populations of anchovy and thread herring which could be used for industrial purposes have been reported from the Gulf of Mexico. These may rival the former menhaden stocks in their potential for an industrial fishery. Exploitation of these stocks might compensate for the drop in menhaden and support the total tonnage curve for a while at least.

The fisheries in international waters are being subjected to intensive exploitation, in this case by foreign as well as by United States fleets. When

European fishermen came to the western Atlantic to fish they started on the rich Grand Banks of Newfoundland. They have worked steadily southward. Today eight nations are fishing on Georges Bank off Cape Cod and some of them are now working off the middle Atlantic states. The Canadians who formerly found all the fish they needed off their own shores, first moved south to Georges Bank and now go as far as the Virginia Capes. As the world demand for protein foods increases the wide ranging foreign fleets will extend their area of operations even further. We can reasonably expect the development of international fisheries along the entire Atlantic and Gulf Coasts.

As the foreign fleets have worked southward, total landings from the offshore waters have increased. This was accomplished primarily by harvesting species which were not previously exploited or were underexploited. Examples are the offshore herring on Georges Bank which were entirely untouched until the Soviets started fishing them in 1961 and the silver hake which were not fully exploited when the same fleet began taking them in 1963. The foreign fishing of some species has been at the expense of United States fisheries. The red hake fishery in the United States, for example, has virtually collapsed since the Soviets started fishing the species two years ago. Likewise, the pulse fishing of haddock during a period of temporary abundance has had a serious effect on the United States haddock fishery.

As the pressure of foreign fleets increases along the Atlantic and Gulf Coasts it is not likely that total tonnage from the offshore waters will increase very much. The area has been intensively explored by Soviet and United States research vessels and no new large bodies of fish have been found. Unless there is some radical change in the ecology of the area we can expect the level of total landings from the offshore waters to remain essentially where it is today.

To be sure, there are many species which could be more intensively fished, especially in the Gulf of Mexico and, as time goes on, new specialized fisheries may develop but in terms of total gross tonnage of all species it is not likely that the offshore waters of the eastern United States will produce substantially more fish than they have in the past.

The challenge for the future in these waters is international management. The New England banks lie within the Convention Area of the International Commission for the Northwest Atlantic Fisheries so the instrument for international management exists for this region. Mesh regulations for some species are already in effect here and limitation of effort and of catch are being considered.

For the Middle Atlantic area the United States and the Soviet Union are holding talks to determine what measures should be taken on a bilateral basis to solve the international fishery problems in this area. If other countries move into these areas the situation will become much more complicated, new agreements will be required to conserve these valuable resources.

Sampling Larval Herring from Tidewaters with Buoyed and Anchored Nets[1]

By Joseph J. Graham and Paul M. W. Venno[2]

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West Boothbay Harbor, Maine

ABSTRACT

Buoyed and anchored nets were evaluated as a method of sampling larval Atlantic herring, *Clupea harengus harengus* Linnaeus, in tidewaters. The method permitted exploratory sampling in areas difficult to reach with towed gear, and provided a large number of samples from predetermined depths without towing from vessels. The nightly variation of catch rates was small under similar tidal conditions, and seasonal changes in larval catches were similar to those determined by towing nets from a boat. The buoyed net also provided information relating the distribution of larvae to tidal currents that could not be readily obtained with towed gear.

INTRODUCTION

To study the early life history of Atlantic herring, *Clupea harengus harengus* Linnaeus, in the Gulf of Maine, larval herring are routinely sampled with nets towed by vessels. We needed more information on the distribution and abundance of the larvae, but increasing the number of samples by towing was not feasible. We were also interested in exploratory sampling in areas inaccessible to towing and studied the application of stationary or buoyed and anchored nets, which utilize the "towing power" of tidal flows (Massman, 1952; Dovel, 1964). The design of the buoyed nets is described in this paper and catches made in 1963–65 are evaluated. We determined the straining or filtering efficiency of the nets, calculated the variation of catch rates for individual stations, and compared the seasonal changes in catch rates with those of towed gear.

DESIGN OF THE BUOYED AND ANCHORED NETS

The nets (Fig. 1) were buoyed at the surface and anchored to the bottom to sample at predetermined depths; flow meters provided a measure of sampling effort. The nets aligned in the direction of flow when fishing and closed when the tide was not flowing. Our design included four triangular wooden vanes, each attached at two corners to a buoyed and anchored line by snap-on connectors (Fig. 1A). A net with a mouth opening of 0.5-m diam was suspended by brackets fastened on each side of the free corner of each vane. The weight of a plastic sleeve connecting the net and codend was sufficient to collapse the net during slack water and prevent escape of the

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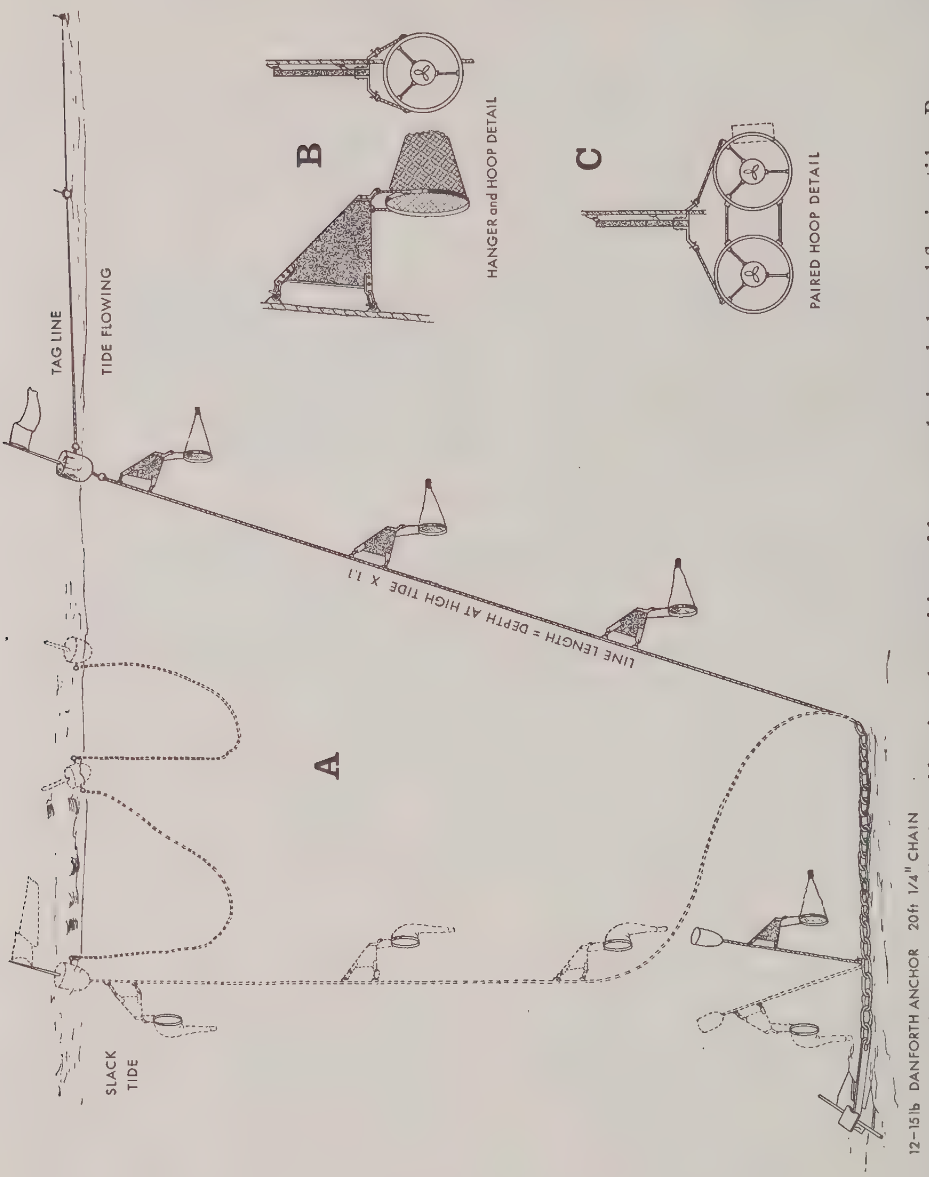
TAG LINE
TIDE FLOWING
B
HANGER and HOOP DETAIL
C
PAIRED HOOP DETAIL
LINE LENGTH = DEPTH AT HIGH TIDE X 1.1
A
SLACK TIDE
12–15lb DANFORTH ANCHOR 20ft 1/4" CHAIN

FIG. 1. Buoyed nets for sampling larval herring. A, positions of four nets during slack and flowing tides; B, arrangement of the hanger and hoop; and C, hoop arrangement for collecting paired samples, with attached board (broken line) used when determining the efficiencies of nets.

catch. When the tide flowed, the nets opened and the vanes aligned the nets in the direction of flow. Ropes attached to the upper sides of each hoop ensured that the mouth opening of the net faced the current. A Rigosha[3] flow meter was suspended at the center of the mouth of each net (Fig. 1B). The impeller of the meter required a minimal current of 3 cm/sec to revolve and the four dials of the meter were capable of recording a total of 100,000 revolutions. One net was fixed near the buoy, two were near mid depth, and another was buoyed by a separate line and float near the anchor. If, when the nets were fishing, the height of the tide exceeded the length of mainline available, the anchor chain rose from the bottom but did not raise the net attached near the anchor. The surface and bottom nets fished at their predetermined positions; the nets near mid depth fished at constant distances below the surface but at varying levels in the water column according to the stage of the tide.

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[3] Rigosha & Co., Ltd., Maruishi Building, Kajicho 1 chome, Kando Chiyoda-Ku, Tokyo, Japan. References to trade names in this publication do not imply endorsement of the products.

EFFICIENCY OF THE NETS

A measure of the volume of water filtered is needed to determine the straining efficiency of the nets. The flow meters were calibrated in meters per revolution of the impeller, over distances of 1.8 and 3.7 km at speeds of 103 cm/sec and 154 cm/sec. The unusually long distances were necessary to simulate the large amounts of water that would pass through the meters during a tidal cycle. The calibrations of individual meters varied from trial to trial for the two distances until we removed the binding coil spring from the impeller shaft. The spring had been installed by the manufacturer to disengage the impeller in periods of no flow. First estimates of the volumes of water strained for each flow meter (area of net mouth × meters per revolution) were from 0.0181 to 0.0214 m^3 per impeller revolution; 1 year later they varied from 0.0184 to 0.0217.

Straining efficiencies of the nets were determined by suspending flow meters in the hoops of the double frame (Fig. 1C). One hoop had a net attached; the other hoop had no net, but a small board was placed on the outside rim to equalize the drag and to help align the vane within the current. The meter with a net attached measured the rate (centimeters/second) of flow through the net, and the meter without a net measured the actual flow surrounding the net. The ratio of the two measurements provided an estimate of the efficiency of the net. Two methods, towing from a vessel and buoying and anchoring the nets in an estuary for 15-min periods, provided us with a range in current velocities expected in tidal waters.

We tested the straining properties of a monofilament mesh and two knitted nylon meshes after extensive use. Mesh apertures were 0.39, 0.74, and 1.02 mm, and the numbers of meshes per centimeter were 19, 9, and 6, respectively. The mesh aperture of the finer of the two knitted nets corresponded to the diameter of a 5-mm yolk-sac larval herring; and that of the coarser net to the diameter of a 20-mm larva. The efficiencies ranged from 80 to 90% at speeds above 30 cm/sec for the monofilament and above 15 cm/sec for knitted meshes; but efficiencies were extremely variable at slower speeds.

Currents less than 15 cm/sec are common in our tidal waters; therefore we investigated the source of these large variations within the smaller meshed (0.74 mm) knitted net. We observed the flow of water through nets suspended from a dock and Scuba divers observed the flow through nets anchored in a channel. The same fluctuations in velocities that occurred within the mouth of the net were present in the surrounding water. They closely resembled the movements of eddies superimposed on an average flow, a characteristic of turbulent flow described by Alberston et al. (1960, p. 217). The similarities in fluctuations in velocities suggested that movement of water through the net was unimpeded at low velocities. Because the orientation and size of the eddies are random in turbulent flow, it would be unlikely that any systematic differences between the amounts of water moving through various portions of the mouth would persist through time (hours). It is suggested that the 15-min period during which the double hoop was buoyed and anchored in the estuary was insufficient to average the variations in velocity. The fluctuations in flow within the mouth of the net would cease when the average velocity (15 cm/sec) caused sufficient friction on the meshes of the net to "organize" the flow of water through the mouth. We concluded that during a flood or ebb tidal current a meter at the center of the net would give a reliable estimate of the total flow through the net.

Because the nets could capture large amounts of plankton over a tidal cycle, we tested the effect of clogged meshes on the efficiencies of the knitted and monofilament nets. Mesh openings were reduced for the tests (1) with plankton captured by the nets and (2) by artificially reducing the size of the cone of each net. The double hoop with one net attached was towed for 0.9, 2.8, and 3.7 km to coat the meshes with particulate (8–155 ml) and jellied (80–350 ml) plankton. Immediately after we collected the plankton the double hoop was towed first at 156 and then 200 cm/sec for 15 min. The nets were then cleaned, one third of each cone was tied off to simulate clogging and the tows repeated for the two speeds. The efficiencies of the knitted nets were not affected; the efficiency of the monofilament net was 80% when the size of the cone was reduced and dropped to 68% when the meshes were clogged.

EXPLORATORY SAMPLING OF 1963–64

Sets of buoyed nets were made to determine whether larval herring could be captured in locations difficult to reach with towed nets. In the autumn of 1963, before our experiments with knitted nets, we began trials in the Sheepscot estuary with buoyed monofilament (aperture 0.39 mm) plankton nets without meters. These sets captured larval herring. During the winter, sets were made in other coastal areas that were difficult to sample with towed gear. The nets captured larval herring in five of the seven estuaries (Fig. 2). The absence of larval herring in catches from estuaries of the Machias and Pleasant rivers during the winter coincided with an absence of larvae in catches of towed gear in the bays adjacent to the mouths of the estuaries.

In the summer of 1964 we made a total of twelve 12-hr sets in the Damariscotta estuary. Paired and metered knitted nets were mounted on the double hoops, at the surface and at 10 m. The nets, 12 pairs at each depth, captured zooplankton and larval fishes other than herring, which are not

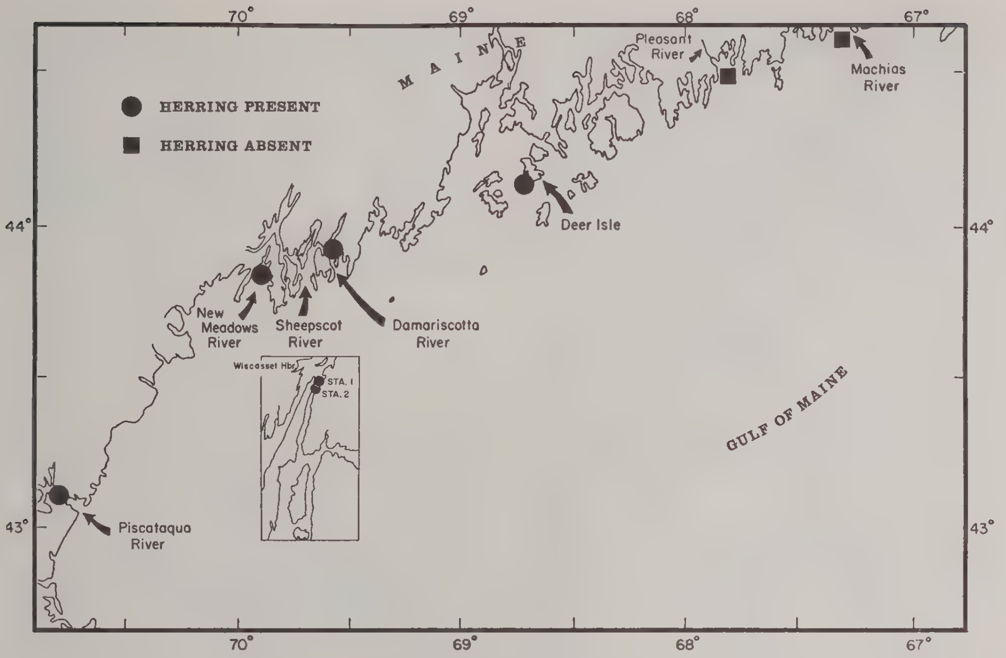
70°
69°
68°
67°
MAINE
Pleasant River
Machias River
● HERRING PRESENT
■ HERRING ABSENT
Deer Isle
44°
44°
New Meadows River
Sheepscot River
Damariscotta River
Wiscasset Hbr
STA. 1
STA. 2
GULF OF MAINE
43°
43°
Piscataqua River
70°
69°
68°
67°

FIG. 2. Exploratory sets of buoyed nets for larval herring along the coast of the Gulf of Maine during the winter, 1963–64.

present in the summer. For each net we counted the fish, measured the displacement volume of zooplankton, and calculated the volume of water strained. The number of larval fish averaged 20 and varied from 1 to 162. Volumes of plankton averaged 36.2 ml and varied from 2 to 90 ml. The amounts of water strained by all of the paired nets differed greatly. But statistical comparison (*t*-test) of catches per 100 m^3 of water strained showed no significant differences for plankton volumes ($P > 0.50$) or larvae ($P > 0.35$) among the 24 catches from both depths.

SAMPLING IN SHEEPSCOT ESTUARY, 1965

CATCH RATES AT TWO STATIONS

In the spring of 1965 we captured larval herring by fishing serially a set of four knitted nets at each of two stations for five consecutive nights in the Sheepscot estuary (Fig. 2). Sufficient distance was allowed between the sets along the estuarine channel to prevent tangling. The channel was 370 m wide and 20 m deep and larval herring were present throughout the experiment. We set the nets and fished them until the next slack tide. During slack tide the nets were retrieved, reset, and a hydrographic cast was made between the stations. The nets were retrieved again at dawn. Ebb tides were fished for $2\frac{1}{4}$–$5\frac{1}{4}$ hr and flood tides for $5\frac{1}{2}$–$6\frac{1}{2}$ hr. The 20 sets (2 each night at each station) captured 14,312 larval fish, including 4025 larval herring. The catches of individual sets varied from 49 to 1002 for all larval fish and from 21 to 444 for herring. Catch per unit effort was calculated for each set of four nets from the total amounts of water strained and total catches of all larval fish and herring (Fig. 3). The amount of water strained increased with the length of time fished and an F-test suggested that the relations for the two stations fitted a common slope ($P > 0.20$). This evidence was sufficient to justify grouping the data from sets at the two stations in pairs and to compare them statistically by a *t*-test. Most catch rates at station 1 were greater ($P < 0.01$) than those at station 2 for all larval fish and for herring.

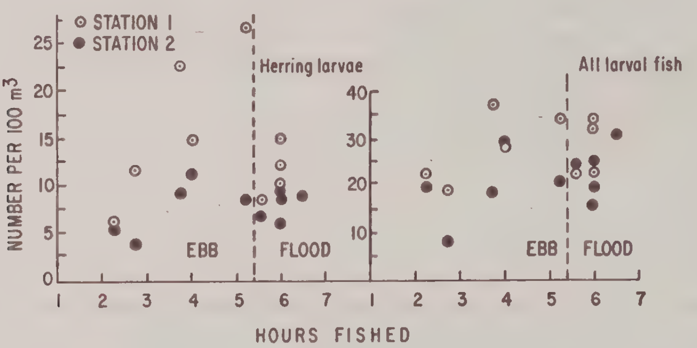

FIG. 3. The relations of the catches of larval fish at two stations to the numbers of hours fished during ebb and flood tides.

EFFECT OF TIDAL EXCURSIONS ON CATCH RATES

The differences between catch rates at stations 1 and 2 were related to changes in tidal current and the distribution of larvae. To examine currents we calculated tidal excursions[4] from the readings of flow meters in each net (flow meter reading × calibration factor in meters/revolution of impeller). Vertical profiles of the excursions were usually typical of those expected in estuaries; excursions were usually longest at 10–15 m on the flood tide and at the surface during ebb tide (Fig. 4). The profiles were similar for the two stations until the fourth and fifth nights of fishing, when they became atypical during the flood tide at station 1. These atypical conditions in the profiles were associated with increased river discharge shown by lowered salinity and increased temperature (Table I). Station 1 abutted a large embayment, which apparently made it more sensitive to alterations of the tidal currents from the addition of fresh water to the estuary.

The depth distributions of catches of larval fish resembled the distributions of tidal excursions. Vertical distributions of larval herring (Fig. 5) frequently showed the greatest numbers of larvae at 10 and 15 m for flood tide and at the surface for ebb tide. The distribution (percentage) of larvae at each depth was correlated with the excursion for both tides at station 2 (flood $r = 0.88$,

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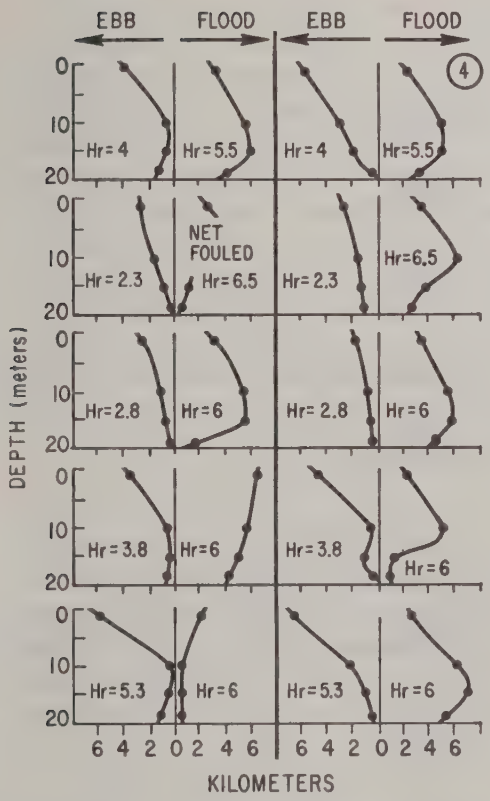
[4] A tidal excursion is the distance a given particle of water moves away from the position of the anchored net during a flood or ebb tide.



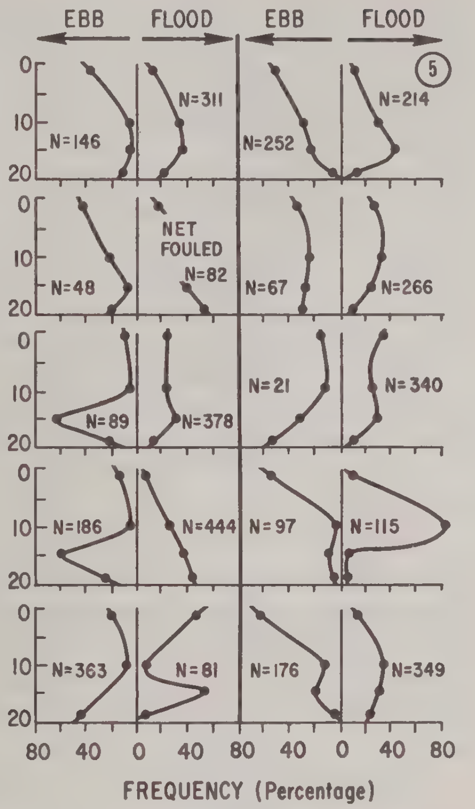


FIG. 4. Profiles of tidal excursions at stations 1 (*left*) and 2 (*right*) in the Sheepscot estuary, arranged in order of consecutive nights of fishing, April 5 (*top*) to April 9 (*bottom*), 1965.

FIG. 5. Depth distributions of larval herring at stations 1 (*left*) and 2 (*right*) in the Sheepscot estuary, arranged in order of consecutive nights of fishing, April 5 (*top*) to April 9 (*bottom*), 1965.

TABLE I. Water temperatures, salinities, and catch rates (numbers/100 m^3) of larval herring (ebb and flood tides combined) for the Sheepscot estuary, April 5–9, 1965.

	Temp (C)								
		Bathythermograph			Salinity (‰)			Catch rates	
Night of operation	Bucket Surface	0 m	10 m	15 m	0 m	10 m	15 m	Station 1	Station 2
1	3.4	3.5	3.8	3.7	29.9	30.5	30.7	9.6	8.7
2	3.4	3.4	3.3	3.1	30.0	30.4	30.8	8.4	8.8
3	4.4	4.3	4.1	3.9	28.3	29.1	29.5	12.2	7.9
4	4.4	4.1	4.2	4.2	28.6	28.9	29.2	12.4	6.6
5	4.5	–	–	–	27.3	28.6	29.3	23.6	8.8

ebb $r = 0.86$, df $= 18$, $P_{.05} = 0.56$) and for the flood tide at station 1 ($r = 0.75$, df $= 14$, $P_{.01} = 0.62$). The correlation for data from the ebb tide at station 1 ($r = 0.49$, df $= 18$, $P_{.05} = 0.44$) was borderline; the numbers of larval herring were large in short tidal excursions on the 3rd–5th nights. This association produced large ratios of catch to volume (m^3) of water strained (42/4.7, 15/2.7, and 97/0.2) during the 3rd–5th night of fishing, when temperature increased and salinity decreased progressively in response to increased river discharge into the estuary. Catch rates at station 1 varied with changes in temperature and salinity but those at station 2 did not (Table I). Perhaps the larger catch rates at station 1 represented an accumulation of larvae during daylight in areas of low tidal velocities where they could await a favorable tide. Creutzberg (1961) described an analogous situation for elvers that move shoreward on the flood tide and then seek bottom to prevent their transport seaward during the subsequent ebb tide.

Sizes of Larvae

The length distributions of larval herring were similar at the two stations. Length frequency plots at station 1 varied little from those at station 2 for a given depth and their modes tended to occur at a slightly larger size at the surface and bottom than at midwater at both stations (Fig. 6). Further, when the data were combined for all depths, the differences in the configurations of the plots between flood and ebb tides were similar in detail at the two stations.

SEASONAL CHANGES IN CATCH RATE IN THE SHEEPSCOT ESTUARY

Larval herring hatch at 5 mm (standard length) in the autumn and metamorphose at 45 mm in the spring. In 1964–65, we towed a 1-m net in the Sheepscot and Damariscotta estuaries (Fig. 2), but it was effective only in the autumn (Graham and Boyar, 1966). We also towed a Gulf III sampler from the period of hatching until the larvae reached a length of 20 mm, and then used an especially designed trawl — the Boothbay depressor trawl (Graham and Vaughan, 1966) — for larger larvae.

From October 1964 through April 1965 we made a series of nighttime sets of buoyed nets in the narrow channel of the Sheepscot estuary, and compared the catches with those obtained concurrently with the gears that were towed within the surrounding area (Fig. 7).

The stationary and towed gears showed the same seasonal increase in lengths of larvae. Catch rates were highest in the autumn, lowest in the winter, and high again in the spring. Catches with towed gears, mostly made during daylight, were much smaller than those made at night with the buoyed nets. Catch rates from individual night tows near stations 1 and 2 in the Sheepscot (Fig. 2) were more comparable with those of the buoyed nets. On March 16, 12.9 larval herring per 100 m^3 were captured with the trawl at night and 56.0 on April 27. During the intervening period April 5–9, individual sets of buoyed nets captured from 3.7 to 27.1 larvae per 100 m^3.

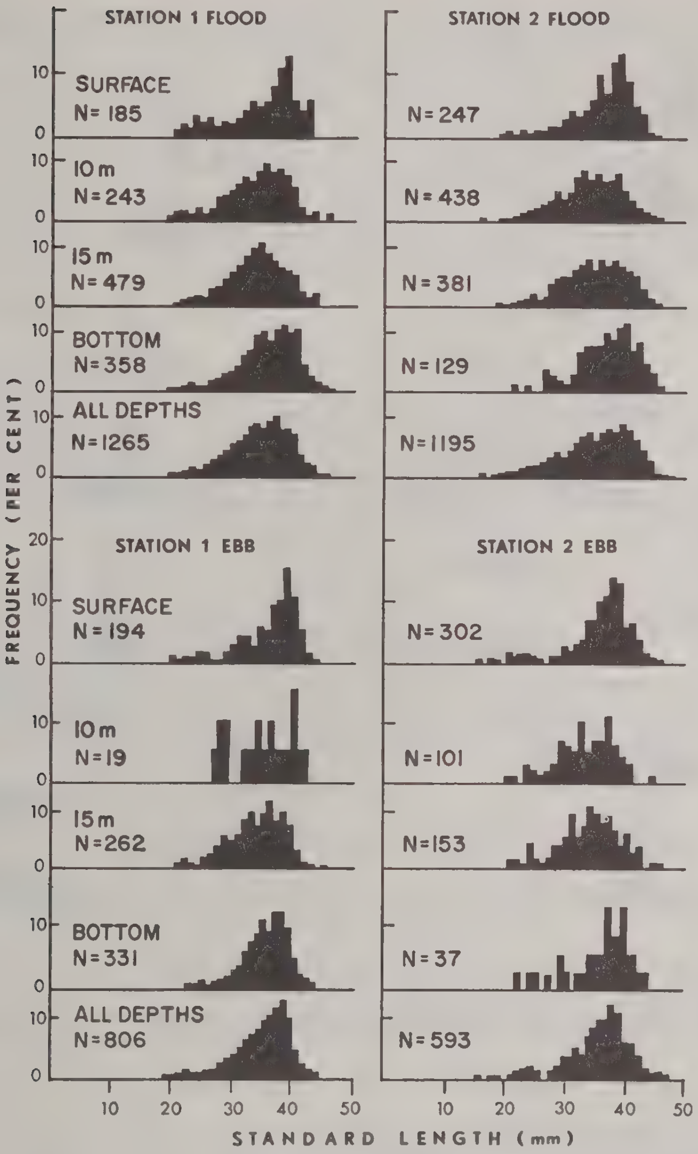


FIG. 6. Length frequencies of larval herring captured during the flood and ebb tides at stations 1 and 2 in the Sheepscot estuary (data combined for five consecutive nights of fishing, April 5–9, 1965).

COMPARISON OF BUOYED AND TOWED NETS AS SAMPLING GEAR

Differences between day and night catches, which are common for herring, result from avoidance of the towed gears by the larvae during the day and their redistribution vertically from day to night (Colton et al., 1961; Dragesund, 1965). The relation between the vertical distribution of the larvae and the

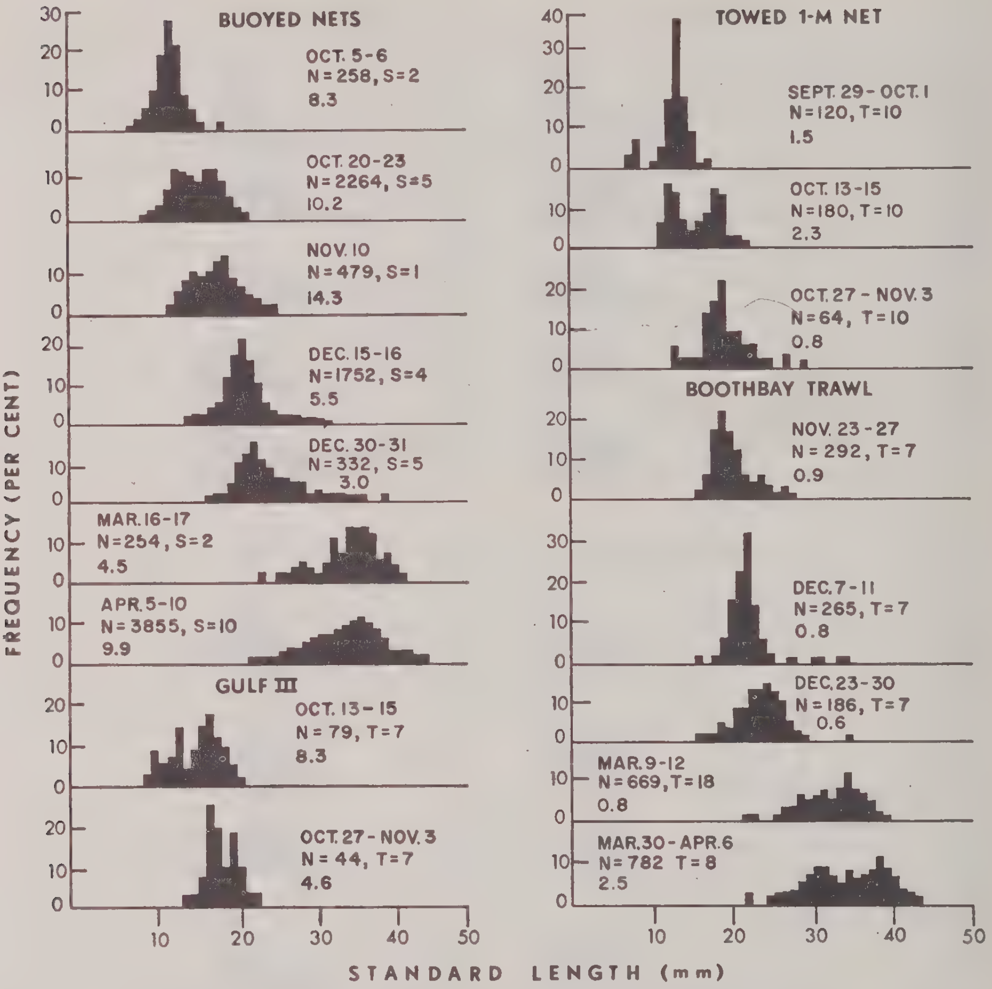


FIG. 7. Comparison of catches of larval herring in buoyed nets with catches in towed gears. N, number of fish; T, number of tows; S, number of sets; and 0.0, catch per 100 m^3.

lengths of the tidal excursions for many of the night sets suggests that (1) larvae were evenly dispersed along the channel of the estuary and (2) avoidance of the net or escapement of larvae was small before the onset of metamorphosis. But avoidance or escapement did apparently occur during daylight. Only one or two larval herring per set were captured in daylight with the buoyed nets, whereas several hundred were taken at night. During the day, the towed gears captured larvae of the same size-range as those captured at night by the buoyed nets. This success in capturing larvae, especially in the spring when they were large, attested to the advantage of the trawl in daytime, and probably was due to a high towing velocity of 206 cm/sec and a larger mouth opening (1 m^2) than that of the buoyed nets.

Towed and stationary gear both have limitations when used to detect changes in the distribution of larval herring over brief periods of time. Hopkins (1963) reported that several tows are necessary at a given station to obtain a representative sample from a single tide with a Clarke–Bumpus sampler. Thus, to sample at a series of stations several times during a tidal cycle requires considerable effort. Since our trawl tows cover about 3.7 km and last 30 min, only a few stations can be sampled during a tide. Buoyed nets can be set to fish "synoptically" over an entire tidal cycle, but the volume of water filtered by buoyed nets is sometimes very small and not comparable with the larger volumes sampled by towed gear.

ACKNOWLEDGMENTS

Our colleagues at the West Boothbay Harbor Biological Laboratory made helpful suggestions on the design of the buoyed nets. Mr George B. Vaughan combined the suggestions into a working model. Scuba divers Richard A. Cooper and Peter A. Henderson observed the functioning of the nets under water.

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Blood Lactate Concentrations and Mortality in Sockeye and Chinook Salmon (*Oncorhynchus nerka* and *O. tshawytscha*) After Exercise[1]

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ABSTRACT

Blood lactate concentrations in 306 sockeye salmon (*Oncorhynchus nerka*), taken at sea in 1965 and 1966 by purse seine, gillnet, and longline, and in 98 starved or fed immature chinook salmon (*O. tshawytscha*) that had been exercised in a saltwater pond were generally below those reported in the literature as related to stress-induced mortality in salmon. No sockeye salmon held in shipboard tanks for observation died within 2 days after capture, although most of the fish died later. Few fish died among starved or fed immature chinook salmon in salt water within 10 days after capture by hook and line or after being chased to exhaustion; blood lactate concentrations in these fish were generally higher than in sockeye salmon after stress but were still usually below the reported critical level of 125 mg/100 ml.

We concluded that neither the adult sockeye nor immature chinook salmon suffered immediate fatigue-related mortality, but the possibility that fatigue could induce delayed mortality was not excluded.

INTRODUCTION

Many reports have been published during the past 30 years on the relation between severe muscular exercise and mortality in fishes; comprehensive reviews appear in Black (1958), Beamish (1966), and Black et al. (1966). Among the salmonids, mortality attributed to muscular fatigue and related stress were reported for chinook salmon (*Oncorhynchus tshawytscha*) by Parker and Black (1959); for coho salmon (*O. kisutch*) by Milne and Ball (1956) and Parker et al. (1959); for sockeye salmon (*O. nerka*) by Black (1957c); and for rainbow trout (*Salmo gairdneri*) by Bouck and Ball (1966). In contrast, no mortalities after severe exercise were reported for chinook salmon by Jensen (MS, 1958); for coho salmon by Paulik et al. (MS, 1957) and Parker et al. (1959); for sockeye salmon by Paulik and DeLacy (MS, 1958); for Kamloops trout (*S. gairdneri*) by Black (1957a); nor for lake trout (*Salvelinus namaycush*) by Black (1957b).

Why mortality occurred in some groups of fish after extreme exercise and not in others has not been clearly shown. Beamish (1966) noted that fatigued coho, chinook, and sockeye salmon that died were in salt water, whereas groups in which mortality was insignificant after severe exercise had

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been starved and were exercised in fresh water. Jensen (MS, 1958), however, observed little mortality in age-II and age-III chinook salmon caught by hook and line in salt water. In immature troll-caught chinook salmon, Parker and Black (1959) demonstrated a positive correlation between mortality and concentrations of blood lactate.

Parker et al. (1959) also reported high blood lactate concentrations and a high mortality for feeding coho salmon captured by ocean trolling. They found also that adult coho salmon displayed neither high mortality nor high concentrations of blood lactate after exertion in fresh water. They concluded that troll-caught coho salmon suffered mortality when blood lactate concentrations exceeded 125 mg/100 ml and remained elevated during holding after capture. However, the specific cause of death may have been acidosis from *p*H changes (Jonas et al., 1962) rather than lactic acid concentration per se.

Factors other than severe injury or fatigue may also be related to mortality or disability of salmonids after capture and handling. Parker et al. (1963), for example, speculated that delayed mortalities may arise from breaks in the epidermis or from scale loss, which result in secondary infections or osmotic imbalance.

Most reports on fatigue-related mortality are concerned with death within several hours of stress (here termed "immediate" mortality). Little work has been done on delayed effects. Milne and Ball (1956) and Bouck and Ball (1966), however, observed delayed mortality (death after more than 1 day) after stress in coho salmon and rainbow trout.

The present studies were initiated to provide information on mortality or disability as a result of stress imposed on salmon during capture and tagging at sea and to define better the mechanisms involved. Sockeye salmon caught on the high seas were sampled to assess the effects of fatigue, as induced under field conditions, on blood lactate levels and mortality. Chinook salmon reared in a hatchery were held in a saltwater pond to determine the incidence of delayed mortality and to compare mortalities of fed and starved fish after known periods of exercise.

METHODS AND MATERIALS

Collection Procedures and Sampling Methods for Sockeye Salmon

Maturing salmon from Bristol Bay, Alaska, were sampled during June and early July of 1965 and 1966 in "offshore" and "inshore" areas (Fig. 1). Our sampling in 1965 was set up to assess the lactate response of sockeye salmon during field tagging procedures. The design was modified in 1966 to include sampling of blood over a longer period after landing and to observe mortality after capture.

Purse seines were used in 1965; each set lasted 30–45 min. Salmon were brailed from the seine and placed in a square plywood tank (4100 liters) supplied with a continuous flow of fresh sea water. Not more than 550 fish were held at any time. Unloading the seine usually took about 10 min. The landing

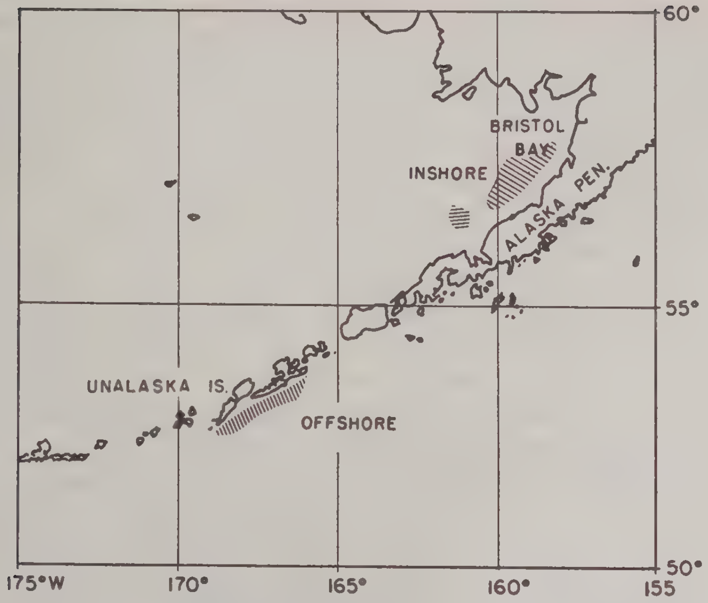

FIG. 1. General sampling locations for Bristol Bay sockeye salmon in 1965 and 1966.

time for a group of fish was taken as the time the first net load was brought on board. Fish to be sampled for physiological studies were dipped out of the holding tank and quickly killed by a sharp blow on the head. A total of 139 fish were sampled from 5 to 140 min after landing; the rest were tagged and released. Blood was obtained by cardiac puncture and collected in sterile tubes without anticoagulant. A 0.5-ml aliquot of whole blood was immediately added to 4.5 ml of cold 10% trichloroacetic acid (TCA) solution and placed at −18 C in a shipboard freezer for subsequent laboratory analysis for lactate. The length, sex, and general condition were then determined for each fish. Surface water temperatures varied from 3.8 to 6.8 C during the sampling period.

Gillnets and longlines were used for capture in 1966, but most blood samples were from fish taken on longlines. The longline gear was fished for 1 hr in all offshore sets and for 1½ hr at the single set made inshore. All but one of the sockeye salmon captured by longline for these studies were alive when landed and appeared healthy and uninjured. As the gear was retrieved, hooks were removed and the fish were placed in a canvas holding tank 1 m in diameter; salt water flowed through the tank continuously and the water was 1 m deep. No more than five fish were in the tank at once.

One of every three sockeye salmon brought on board was killed and blood was collected as in 1965, except that an anticoagulant (ammonium heparin) was used; a total of 71 fish were sampled. An aliquot of each blood sample was placed in TCA for lactate determinations; the remainder was centrifuged and plasma collected for other studies. The other fish caught were tagged with Petersen discs and placed in one or the other of two steel holding tanks (each 0.9 × 2.1 × 0.75 m deep) through which a constant flow of fresh sea water was pumped to ensure adequate aeration. Ocean surface water temperatures varied from 3.8 to 6.3 C. The fish (96) from one tank were killed from 2 to 6 hr after landing and sampled as above. The remaining 39 fish were held for mortality estimates.

Samples for blood lactate determinations were taken from three other groups of fish. Four sockeye and 10 chum salmon (*O. keta*) caught by longline were held and the same individuals bled repeatedly for blood lactate determinations; in this serial sampling, blood was taken from the ventral aorta where possible, or otherwise from the heart. These fish were placed in a tagging cradle, ventral side up, and manually held. No difficulty was experienced and most samples were obtained within 20 sec. The second group was composed of 25 sockeye salmon which had been held for 3–52 hr for mortality studies. These fish were severely stressed by accidental draining of the holding tank because of water pump failure; they struggled intensely, lost many scales, and most were motionless by the time the water was restored 20 min later. All fish subsequently revived, but a few failed to maintain an upright position. All were killed and sampled for blood lactate $1\frac{1}{2}$–2 hr or $3\frac{1}{2}$–$4\frac{1}{2}$ hr after the water supply failed. The third group of fish for which blood lactates were determined consisted of 17 gillnetted sockeye salmon; these fish were initially selected because they appeared to be vigorous and uninjured and were placed in the steel holding tanks to recover. After 12–14 hr or 36–38 hr, the fish were killed and blood samples taken.

Blood lactate was determined by the colorimetric method of Barker and Summerson (1941), as outlined in Oser (1965, p. 1102–1105). Repeated determinations (27) made on a standard solution (50 mg/100 ml lithium lactate) established that this technique was accurate (range, 44.9–54.2 mg/100 ml). The maximum range of values from multiple bleedings of 10 sockeye salmon was ±5.4 mg/100 ml around the mean.

Sampling Procedures for Chinook Salmon

Fall chinook salmon of the 1964 year-class from hatcheries on the lower Columbia River were transferred to salt water at the Bowman's Bay marine station of the Washington State Department of Fisheries in June 1965. The fish, which ranged from 23 to 37 cm fork length, were fed Oregon moist pellets three times a week. Water temperatures ranged from 6 to 9 C. Mortality, mainly of precocious males, was about 3% during November 1966; our experiments were conducted in December 1966.

The fish were herded without handling into partitioned areas of a pond (Fig. 2), where they were separated into fed and starved test groups (to be exercised) and a control group (to be fed, but not exercised). The two test groups contained about 60 fish each, the control group over 200. Fish in our first experiment were fatigued by capture on hook and line. The procedure

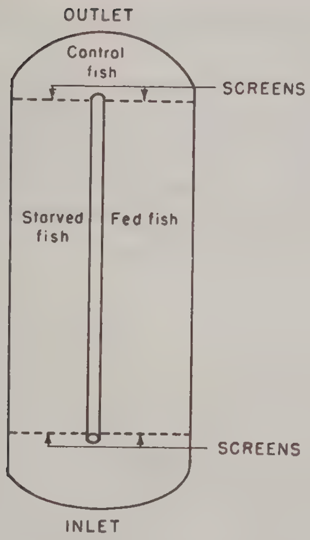

FIG. 2. Diagrammatic view of saltwater rearing pond (6 × 24 m) in which chinook salmon were tested.

was similar to that used by Jensen (MS, 1958) except that our fish were tagged instead of finclipped. Fourteen fish (8 fed, 6 starved) were caught, tagged with Petersen discs, and released. In later experiments, water in the pond was lowered to 7–8 cm; the fed and unfed test groups in the two raceways were then simultaneously chased to exhaustion (18 min) and could be picked up easily.

Twelve fish from each exercised test group were tagged and returned to the water, which was restored to a depth of about 1 m, to assess the combined effects of exercise and tagging; the remaining 40–42 fish from each test group were left untagged to determine the effects of exercise alone. The water level for the control group (about 200 fish) was never lowered below 0.3 m in the well at the end of the pond, where they were disturbed as little as possible. Mortalities for the three groups were monitored for 10 days after exercise by daily inspection and carcass collection.

In a later experiment, 60 fish were taken randomly from the 280 control and remaining test fish (those that were chased but not handled or tagged) of previous experiments. These 60 fish were separated and chased to exhaustion as before. About half were killed for blood lactate determinations at intervals of 1½–2 hr and 5–5½ hr after they had been chased. The rest were held and mortality observed. An unexercised group of 22 fish was also sampled to determine blood lactate concentrations while at rest.

EFFECTS OF STRESS

BLOOD LACTATE IN SOCKEYE SALMON

For two groups of sockeye salmon caught by gillnets and held in shipboard tanks, blood lactate values 12–14 hr after capture (12.6 ± 1.10 mg/100 ml; $n = 10$) were similar to those after 36–38 hr (9.6 ± 1.34 mg/100 ml;

$n = 7$). These results are consistent with resting values previously reported for salmon (Black, 1957c).

Initial blood lactate concentrations of 139 sockeye salmon sampled from 5 to 130 min after capture by purse seine (Fig. 3) were only slightly higher (13–18 mg/100 ml) than resting values (9–12 mg/100 ml). The concentrations for fish caught offshore rose to 42 mg/100 ml after 110 min, whereas those of inshore fish rose to 30 mg/100 ml of blood. For both groups the concentrations after 110 min were more than double the initial values.

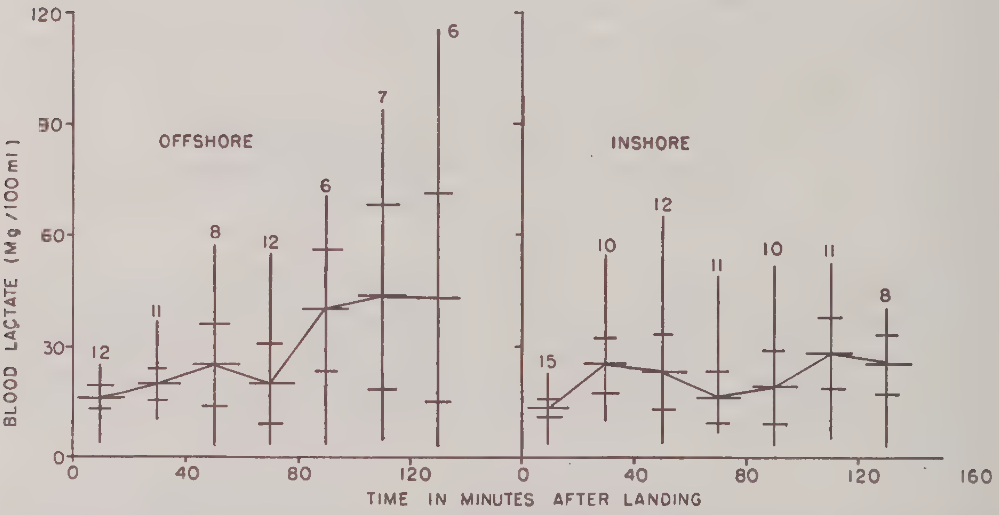

FIG. 3. Blood lactate concentrations in sockeye salmon captured by purse seine in 1965. Vertical bar shows total range; short horizontal bars above and below the mean show upper and lower 95% confidence limits; number above vertical bar shows number of fish in sample.

Blood lactate concentrations of 167 fish, captured by longline and sampled up to 380 min later (Fig. 4), were 2–5 times as high as the values for fish captured by purse seine at comparable times. In offshore fish, the initial concentration of about 50 mg/100 ml increased to 75 mg/100 ml after 140 min and subsequently declined toward resting values after 300 min. The inshore fish had higher initial blood lactate concentrations (62 mg/100 ml) than the other groups studied and the subsequent values were generally higher; however, the values were approaching resting levels after 380 min. These higher concentrations in fish sampled inshore probably reflected more severe weather conditions during sampling than were experienced at other times.

Mean concentrations of blood lactate in 25 sockeye salmon that were severely stressed by draining the tank (Table I) were higher (136-141 mg/100 ml) for fish held only a short time after capture before secondary stress than for fish allowed longer periods of recovery (71–94 mg/100 ml). These results agree with observations on the additive effects of repeated stress on blood lactate concentrations in rainbow trout reported by Stevens and Black (1966).

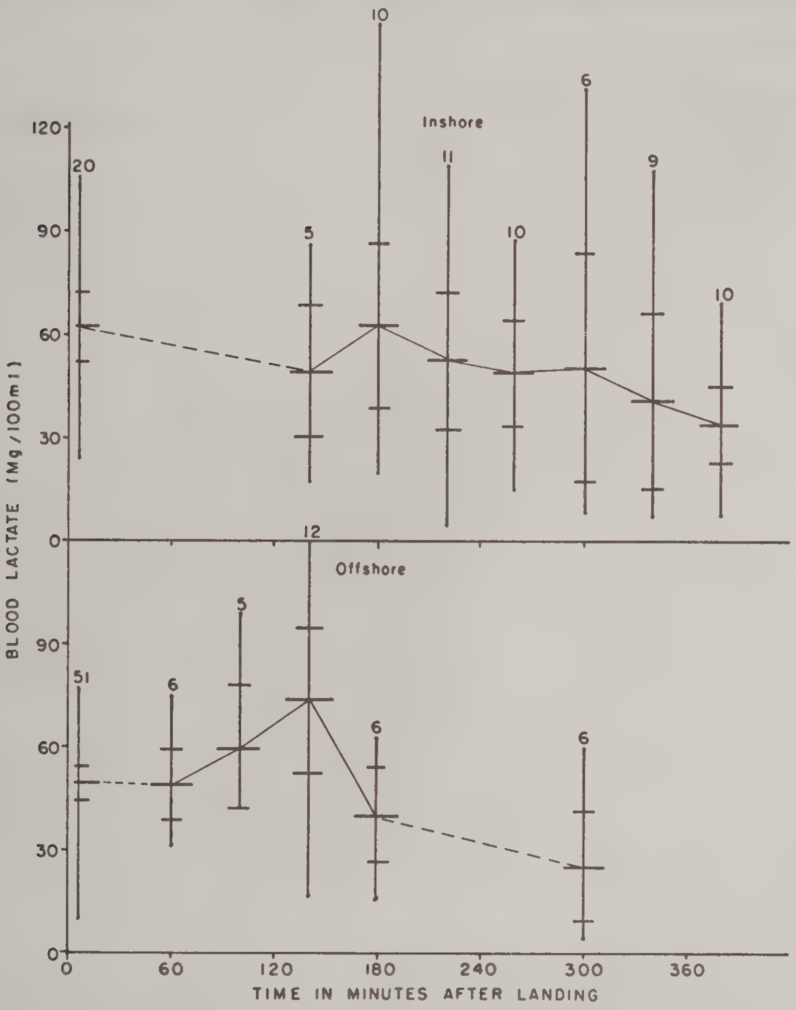

FIG. 4. Blood lactate concentrations in sockeye salmon captured by longline in 1966; broken line indicates incomplete data. Vertical bar shows total range; short horizontal bars above and below the mean show upper and lower 95% confidence limits; number above vertical bar shows number of fish in sample.

Lactate concentrations from serially bled fish captured by longline (Table II) were 60–120% higher for chum than for sockeye salmon in blood taken more than 1 hr after capture. Because the conditions of stress were similar, this may indicate a difference between species. The added stress of serial bleeding is not reflected in blood lactate concentration as these values for sockeye salmon were consistently near or below those for singly bled fish at comparable times (Fig. 4).

TABLE I. Effects of stress from draining shipboard holding tank on levels of blood lactate in maturing sockeye salmon.

Hours spent by fish in tank before draining	Hours after draining and refilling tank before sampling	No. of fish	Blood lactate (mg/100 ml) mean ± SE
3–4½	1½–2	7	141±10.4
3–4½	3½–4½	7	136±21.1
27–52½	1½–2	5	94±4.0
27–52½	3½–4½	6	71±7.6

TABLE II. Levels of blood lactate from serial bleedings of maturing sockeye and chum salmon held in shipboard tanks.

Species	No. of fish	Time of blood sample collection (*hr after capture*)	Blood lactate (mg/100 ml) mean ± SE
Sockeye			
	4	0–¼	41.2±6.08
	4	2–3¼	51.5±13.48
	4	5¾–11¼	13.3±4.06
Chum			
	10	0–¼	41.1±4.78
	10	1–3½	81.6±13.62
	9[a]	5¼–9¼	28.8±7.91

[a] One fish died after 3½ hr.

MORTALITY IN SOCKEYE SALMON

No mortality occurred within 48 hr in sockeye salmon held in shipboard tanks (Table III). Mortality began after 2 days but was probably caused by shipboard holding. The development of numerous surface lesions on these fish after 2 days indicated that disease was associated with the mortality. Fish captured inshore died more rapidly than those captured offshore, but this difference may have been a result of greater stress caused by rougher seas at the inshore station.

BLOOD LACTATE AND MORTALITY IN CHINOOK SALMON

Within 10 days after exercise two tagged test fish caught by hook and line and two control fish had died (Table IV). One of the tagged fish that died received a severe hooking injury and did not recover; the other died 2 days after exercise. Both of the dead control fish were precocious males.

Blood lactate concentrations of exercised and unexercised chinook salmon (Fig. 5) were typical of those reported in the literature cited previously: mean

TABLE III. Mortalities of maturing sockeye salmon captured by longline and held in shipboard tanks.

	Inshore		Offshore	
Days after capture	No. dead	Cumulative mortality (%)	No. dead	Cumulative mortality (%)
0	0	0	0	0
1	0	0	0	0
2	0	0	0	0
3	4	16	0	0
4	8	48	1	7
5	2	56	0	
6	0	56	0	
7	10	96	0	
8	0	96	0	
9	1	100	1	14
10			1	21
11			0	
12			3	43
13			0	
14			0	
15			0	
16			2	57
17			2	71
18			0	
19			0	
20			1	79
21			0	
22			0	
23			0	
24			2	93
25			0	[a]
Totals	25	100	13	93

[a] One fish alive on 25th day.

concentration rose to 110 mg/100 ml about 2 hr after exercise and then declined about 5 hr after exercise. Concentrations were extremely high in a few individuals, but none died within 3 days after exercise.

RELATIONS BETWEEN STRESS, BLOOD LACTATE, AND MORTALITY

These studies indicated that in maturing Bristol Bay sockeye salmon in the marine environment the blood lactate response to stress was similar in timing to that reported for other Pacific salmon. But the concentrations attained under the conditions imposed were below those in troll-caught oceanic chinook and coho salmon which experienced stress-related mortality (Parker

TABLE IV. Mortalities of 2–2½-year-old chinook salmon after different types of stress.

No. of fish	Stress: Nature	Stress: Days after feeding	Stress: Duration (*min*)	No. of deaths within 10 days
8	Hook & line + tagging	1	3.7–6.5	0
6	Hook & line + tagging	8	2.5–5.0	2[a]
12	Chasing + tagging	1	18	0
12	Chasing +tagging	15	18	0
40	Chasing	1	18	0
40	Chasing	15	18	0
200	None	1		2[b]

[a] One fish suffered severe hooking injury and did not recover; the other died 2 days after hooking and tagging.

[b] Both fish that died were precocious males.

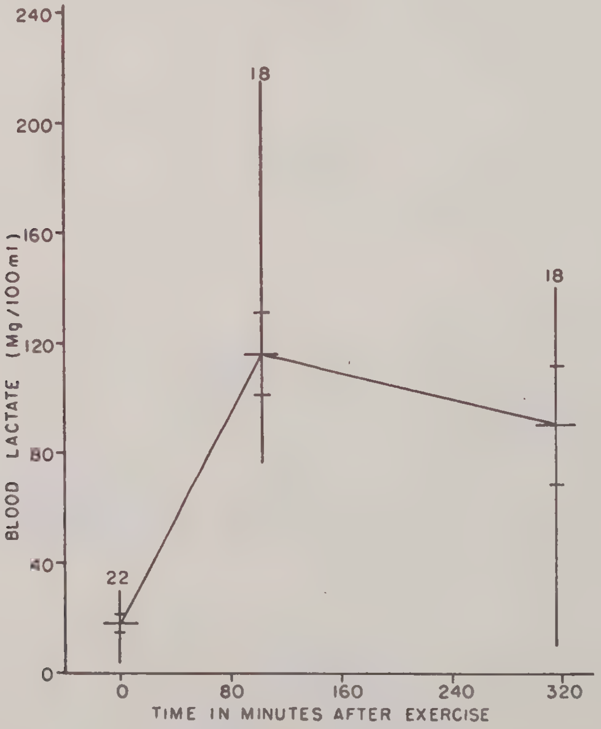

FIG. 5. Blood lactate concentrations in non-exercised chinook salmon and in those chased to exhaustion. Vertical bar shows total range; short horizontal bars above and below the mean show upper and lower 95% confidence limits; number above vertical bar shows number of fish in sample.

and Black, 1959; Parker et al., 1959). Immediate mortality did not occur in the present studies. Possibly the levels or types of stress imposed were not comparable.

Bristol Bay sockeye salmon, if subject to sufficient stress, were shown (Table I) to be capable of developing the concentration of blood lactate designated as critical (125 mg/100 ml) by Parker et al. (1959). Even after the severe trauma experienced by fish when the holding tank was drained, however, no fish died before we sampled for lactate $1\frac{1}{2}$–$4\frac{1}{2}$ hr later.

Examination of stomachs confirmed that the inshore and offshore groups of sockeye salmon were actively feeding. The observed lack of deaths cannot be related, therefore, to cessation of feeding.

The series of experiments performed on chinook salmon in the saltwater pond failed to demonstrate that mortality, either immediate or delayed, was associated with exercise or handling in either starved or fed fish. Blood lactate concentrations were higher than those observed in Bristol Bay sockeye salmon, but were still generally below the critical levels reported elsewhere.

The stress of capture and tagging, therefore, caused no immediate mortality in any of the salmon groups we studied. The delayed deaths of sockeye salmon in shipboard tanks conceivably could have been caused by the stress of initial capture instead of confinement, but we found no delayed mortality in pond-reared immature chinook salmon. The results of pond experiments on immature fish of one species, however, are not necessarily valid for maturing salmon of another species on the high seas.

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Roles of Olfaction and Vision in Choice of Spawning Site by Homing Adult Chinook Salmon (*Oncorhynchus tshawytscha*)[1]

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ABSTRACT

An experiment was conducted to examine the roles of olfaction and vision in directing the choice of spawning site by homing adult chinook salmon (*Oncorhynchus tshawytscha*) on the lower Columbia River. Male fish that voluntarily entered the Spring Creek National Fish Hatchery were treated to occlude their olfactory or visual senses or both. Treated and untreated (control) fish were released upstream and downstream in the river, more than 19 km from the hatchery. Effects were assessed by analyzing returns to the hatchery and to other points.

Of 866 fish released, 348 or 40% were recovered; about half of them, or 176 returned to Spring Creek. Three per cent of the olfactory occluded, 23% of the visually occluded, and 46% of the control fish returned to Spring Creek. Of the fish recovered elsewhere, 77% were recovered at hatcheries and spawn-taking sites along the lower Columbia; 23% were recovered from sources unrelated to spawn taking.

Olfaction appeared to be the key sense that directed the return of these fish to Spring Creek; vision was held to be less important. Olfactory occlusion also reduced the recoveries at other spawn-taking sites, where blinded fish were recovered in appreciable numbers. Recovery of the control fish, especially the smaller ones, at other spawn-taking sites was associated with advancing sexual maturity.

INTRODUCTION

Adult salmon (*Oncorhynchus* spp.), after feeding and growing in widespread areas of the Pacific Ocean, typically migrate back to their native rivers and spawn in their natal waters. Dams or diversions created by the development of water resources can radically change the courses of rivers, confluences of tributaries, qualities of the flowing water, or other possible guideposts in these homing journeys. To foresee the effects of such changes on homing, a better understanding is needed of the mechanisms by which salmon are directed in their migrations — particularly of the sensory responses that guide the fish in those final stages when they choose specific spawning sites.

A favored premise is that final homing is based on olfaction, which enables salmon to detect distinctive odors in the waters originating from their destinations (Hasler and Wisby, 1951). An early experiment on the role of olfaction in homing of sockeye salmon (Craigie, 1926) was inconclusive. From more recent experiments, Wisby and Hasler (1954), using adult coho salmon (*O. kisutch*), concluded that olfactory occlusion interfered with ability to repeat a choice between two tributaries of a small stream and that olfaction enabled the fish to detect distinctive odors of the tributaries.

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We conducted our experiment on the lower Columbia River in the fall of 1960 to test the hypothesis that olfaction plays a decisive role in the choice of spawning sites by homing adult chinook salmon (*O. tshawytscha*) in a large river where the fish may face a number of alternatives. We also examined the role of sight in their choices. As did Wisby and Hasler, we occluded the sensory receptors of fish that had reached a spawning goal, displaced the fish, and then observed their sites of recovery.

EXPERIMENTAL PROCEDURES

Our work centered at the Spring Creek National Fish Hatchery, Underwood, Wash. (Fig. 1) on the main stem of the Columbia River, about 32 km above Bonneville Dam and about 256 km from the sea. Though the hatchery is situated on the river, its source of water for incubation and rearing is a series of adjacent springs. The same spring water fills the holding pond and flows out through a short fish ladder directly into the Columbia River — a physical arrangement suggesting that return of fish to this site may involve discrimination of a specific odor or other water property. The spring water flows from the entrance of the fish ladder at about 0.3 m^3/sec; during our experiment, the mean flow of the Columbia River was about 3000 m^3/sec (U.S. Army Corps of Engineers, MS, 1960).

All fish used in our study were adult males not needed in the normal spawning operation. These fish were captured, anesthetized with tricaine methanesulfonate (M.S. 222), marked with serially numbered disc tags, treated, and released on the same day they entered the hatchery fishway. One of four treatments was used on each fish: (1) olfactory occlusion; (2) visual occlusion; (3) olfactory and visual occlusion; and (4) control (no sensory occlusion, same handling procedures).

Our purpose in using visual occlusion (in addition to testing the role of sight in final homing) was to compare the fish with olfactory blocking with a group deprived of the use of a different major sensory organ in the event that shock from sensory loss alone altered behavior. The purpose of the combined treatment was to check the possibility that fish with olfactory occlusion might follow other migrants by sight and thereby obscure interpretation of the data.

To minimize effects of injury and to lessen the time required for treatment, we selected techniques which would block the reception of external stimuli rather than destroy sensory tissues. Olfactory occlusion was accomplished by packing petroleum jelly and cotton into the olfactory sac and suturing across the nares to retain the plugs. Visual occlusion was achieved by surgical removal of the optic lenses, which were replaced with an opaque mixture of petroleum jelly and carbon black to restrict the entrance of light. Treatment time was slightly over 1 min for olfactory occlusion and less for visual occlusion.

Although these methods did not eliminate the sensory organs, procedures that would have done so seemed unnecessarily severe. The destruction of

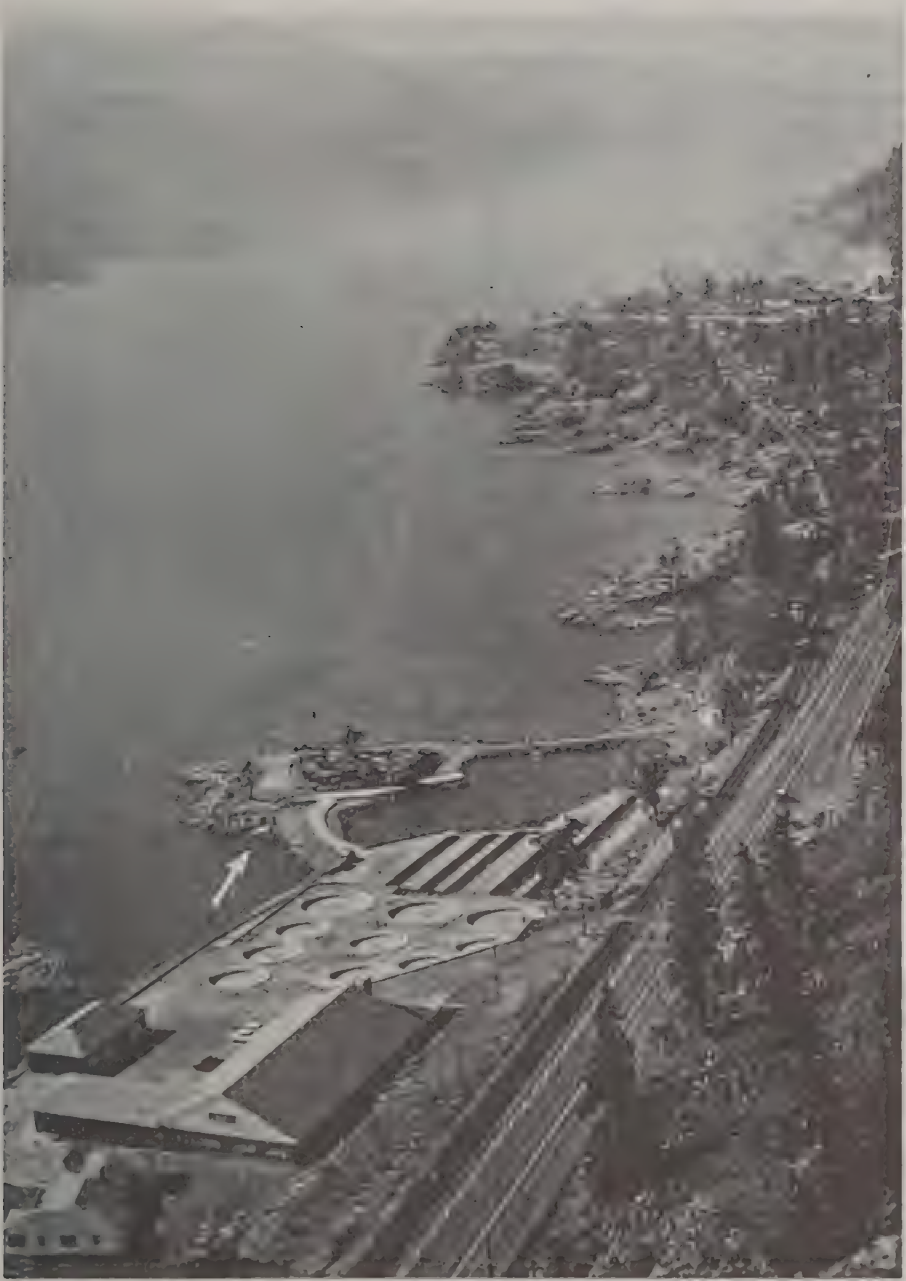

FIG. 1. Downstream view of the Columbia River with Spring Creek National Fish Hatchery in foreground. Holding pond for returning adult salmon is separated from river by earthen dikes; arrow points to water discharge of about 0.3 m³/sec from entrance of small fishway which provides access to the pond.

either sense by severing of nerves would have required deep cuts; the removal of sensory tissue also appeared injurious. Chemical treatment was considered, particularly for destroying sight, but was rejected. Gunning (1959) found that intraocular injections of phemerol to destroy the sight of longear sunfish *Lepomis megalotis* (Rafinesque) caused gross behavioral changes and high mortality. Preliminary tests of our techniques indicated no adverse effects.

After treatment and while still anesthetized, equal numbers of fish subjected to the various forms of treatment were transported by tank trucks to release points away from Spring Creek. We released 866 treated and untreated fish at three sites during September 3–20, 1960. These sites (Fig. 2) were: (1) downstream on the north shore of the Columbia River at Stevenson, Wash.; (2) downstream on the south shore at Cascade Locks, Ore.; and (3) upstream on the north shore at Lyle, Wash. Our purpose in releasing fish at more than one place was to offset the possibility that released fish might return to Spring Creek by retracing their previous routes. All sites were more than 19 river km from the hatchery. Proportional numbers of fish from each treatment group and the control group were released daily at each site, so that the effects of advancing sexual maturity could not confound the results. Also, releases were staggered in time each day to offset the possible effects from unknown factors that might vary within the day.

EFFECTS OF OLFACTORY AND VISUAL OCCLUSION

Tags were recovered at the Spring Creek hatchery, and at other hatcheries or spawn-taking sites, from such activities as sport fishing upstream and downstream from Spring Creek, and from the commercial fishery below Bonneville Dam. A few tags were returned from widely scattered points in the Columbia River and its tributaries.

Tags were recovered from 348 fish (Table I), or 40% of the 866 released. About half (176) of the tag recoveries were fish that returned to Spring Creek National Fish Hatchery.

Returns to Spring Creek

Most of the tags from the Spring Creek hatchery were collected during spawn taking and the dates of return to the hatchery were not known. Tags from the fish that returned from September 4 through 20 were recovered when the fish first re-entered the hatchery fishway from the Columbia River. We examined these fish individually for retention of olfactory plugs and general physical condition. After September 20 (when the releases were ended), hatchery operations precluded recovery and examination of individual fish.

About 50% of the control fish returned to Spring Creek from each of the downstream sites and 37% from the upstream site (Table I). About half as many blinded fish as control fish returned from each release point.

Six fish with olfactory occlusion returned — five from the downstream release site on the north shore and one from the downstream release site on

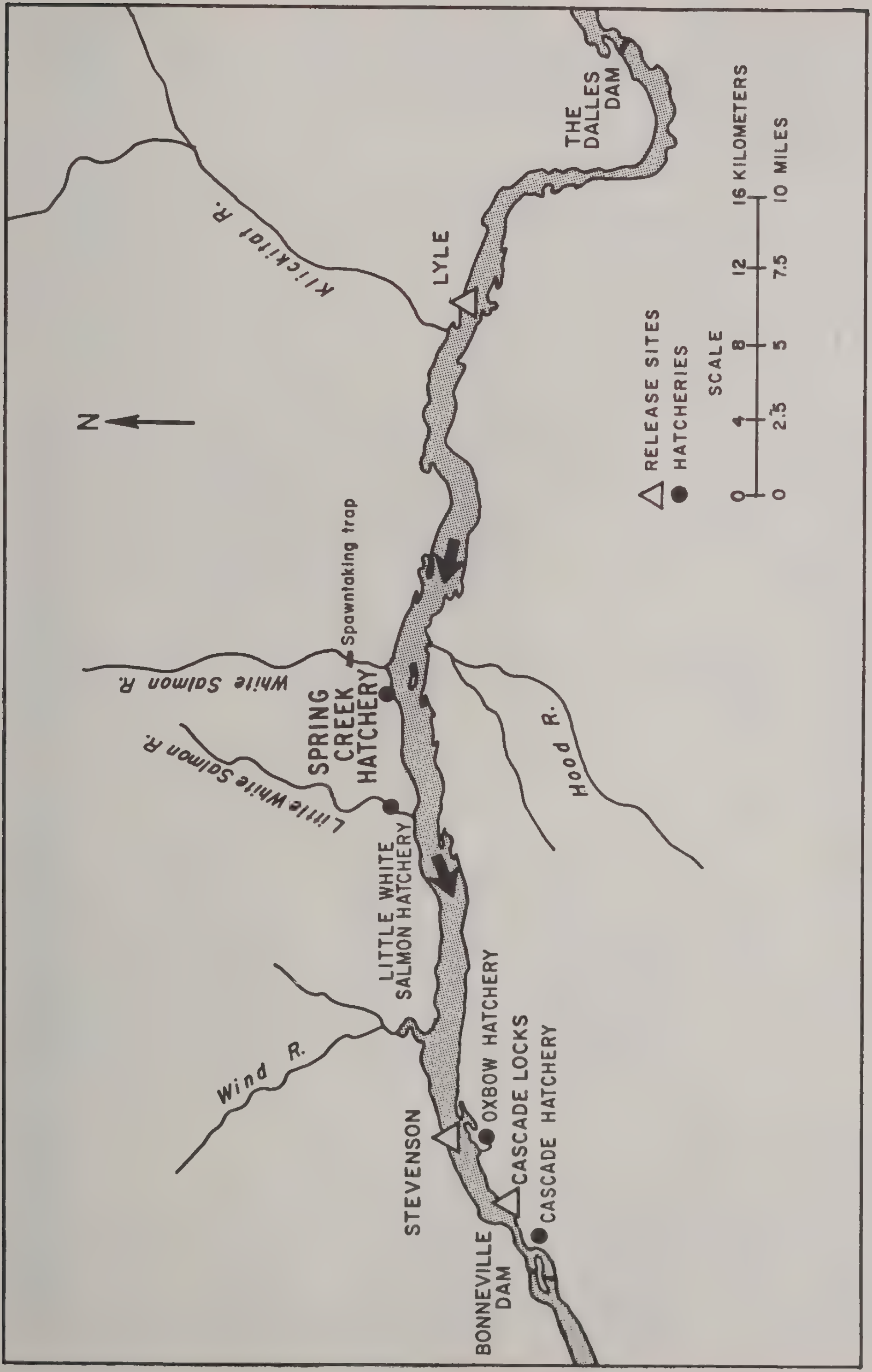
THE DALLES DAM
LYLE
Klickitat R.
N
Spawntaking trap
White Salmon R.
SPRING CREEK HATCHERY
Little White Salmon R.
LITTLE WHITE SALMON HATCHERY
Hood R.
Wind R.
STEVENSON
OXBOW HATCHERY
CASCADE LOCKS
CASCADE HATCHERY
BONNEVILLE DAM
△ RELEASE SITES
● HATCHERIES
SCALE
0 4 8 12 16 KILOMETERS
0 2.5 5 7.5 10 MILES

FIG. 2. Locale of homing experiment on Columbia River.

TABLE I. Numbers of fall-run chinook salmon recovered, September 4–October 11, at various sites on lower Columbia River after displacement to three sites from Spring Creek hatchery and blocking of sensory receptors.

Release site	Recovery site	No. of recoveries, by treatment				
		Olfactory occlusion	Visual occlusion	Olfactory and visual occlusion	Control fish	Totals
		(75)	(96)	(74)	(96)	(341)
Downstream from Spring Creek on north shore of Columbia River at Stevenson, Wash.	Spring Creek Hatchery	5	22	1	48	76
	Oxbow Hatchery	1	11	–	9	21
	Cascade Hatchery	6	2	–	2	10
	Little White Salmon Hatchery	–	1	–	5	6
	White Salmon River	–	7	–	1	8
	Other spawn-taking sites[a]	1	2	–	–	3
	Other than spawn taking[b]	8	–	7	1	16
	Totals recovered	21	45	8	66	140
		(77)	(96)	(76)	(96)	(345)
Downstream from Spring Creek on south shore of Columbia River at Cascade Locks, Ore.	Spring Creek Hatchery	1	24	1	46	72
	Oxbow Hatchery	3	14	–	23	40
	Cascade Hatchery	15	4	1	4	24
	Little White Salmon Hatchery	–	2	–	–	2
	White Salmon River	–	4	–	1	5
	Other spawn-taking sites[a]	1	4	–	–	5
	Other than spawn taking[b]	8	–	8	–	16
	Totals recovered	28	52	10	74	164
		(41)	(49)	(41)	(49)	(180)
Upstream from Spring Creek on north shore of Columbia River at Lyle, Wash.	Spring Creek Hatchery	–	10	–	18	28
	Oxbow Hatchery	–	–	–	–	–
	Cascade Hatchery	1	–	–	–	1
	Little White Salmon Hatchery	–	–	–	–	–
	White Salmon River	–	3	–	1	4
	Other spawn-taking sites[a]	–	1	–	2	3
	Other than spawn taking[b]	2	2	3	1	8
	Totals recovered	3	16	3	22	44
Grand total:	Released	(193)	(241)	(191)	(241)	(866)
	Recovered	52	113	21	162	348

[a] Kalama River Hatchery, Bonneville Hatchery, and spawn-taking facilities on the Klickitat River.
[b] Most recoveries were from sport fishermen and from the commercial fishery below Bonneville Dam.

the south shore. Two fish with visual and olfactory occlusion returned — one from each downstream release point. These eight fish were recovered after September 20 and hence were not examined for retention of olfactory plugs.

Only controls and blinded fish returned from the upstream release site. Of the 482 fish released from all sites without olfactory occlusion, 168, or 35%, returned to Spring Creek; of the 384 released with olfactory occlusion (191 also blinded), however, only 8 (2%) returned.

Fish that returned to Spring Creek from September 4 through 20 were from the control and blinded groups only, but this provided some data on elapsed time between release and return to Spring Creek (Table II). The mean time was about 5 days for control fish and 7 days for blinded fish. No blinded fish returned in less than 4 days, but 10 control fish reappeared within 3 days.

TABLE II. Numbers of control (C) and blinded (B) fish that returned from three release sites to Spring Creek hatchery from September 4 to 20, according to number of days after release.

Days out	No. of fish returning from release sites							
	Stevenson, Wash.		Cascade Locks		Lyle, Wash.		Total	
	C	B	C	B	C	B	C	B
1	–	–	1	–	–	–	1	–
2	–	–	1	–	2	–	3	–
3	4	–	2	–	–	–	6	–
4	6	2	4	–	–	–	10	2
5	2	1	5	1	1	–	8	2
6	1	2	6	1	3	2	10	5
7	2	1	3	2	–	1	5	4
8	2	2	1	3	–	–	3	5
9	–	1	–	1	–	–	–	2
10	–	–	1	–	–	1	1	1
11	1	–	–	1	–	–	1	1
12	–	–	–	–	1	–	1	–
Total fish	18	9	24	9	7	4	49	22
Mean days out							5.5	7.0

The return to Spring Creek of numerous control and blinded fish from all release points, but of few fish with olfactory occlusion, indicated that the return was accomplished more by an olfactory response than by a visually guided retracing of previously traveled routes. The return of only control and blinded fish from the upriver releases additionally suggested the role of olfaction as an orienting mechanism. If fish released upstream had moved back down the river far enough to pass Spring Creek, perhaps only those without olfactory occlusion (control and blinded fish) were able to perceive odors from the hatchery and thereby to respond by re-entering the fishway. Taft and Shapovalov (1938) reported downstream movements of fish that had bypassed their homestream spawning site. Possibly the change in behavior they observed was the result of loss to the fish of orienting odor cues from their home waters.

Fish with olfactory occlusion that returned from downstream may have done so because of ineffective treatment, but on the other hand, their return may have reflected the locations of their release points. Of the eight fish with olfactory occlusion that returned to the hatchery, six were from the north-shore release site on the same side of the river as Spring Creek; these fish may have followed along the shoreline as they traveled upstream. A tendency of migrating adult salmon to orient near the shoreline in the lower Columbia River was reported by Johnson (1960).

Similar ratios between control and blinded fish that returned to Spring Creek from the three release sites (Stevenson, 48:22; Cascade Locks, 46:24; and Lyle, 18:10) suggested that, in contrast to the dominant role of olfaction, vision had a secondary role in the return. The blinded fish were handicapped during their return trip; this fact was indicated by fewer recoveries, delay, and a usually battered appearance on arrival at Spring Creek. They nevertheless reappeared from each release site in appreciable numbers, whereas few unblinded fish with blocked olfactory organs returned.

RECOVERIES AT OTHER LOCATIONS

Of 172 tags recovered from points other than Spring Creek, 132 (or 77%) were from hatcheries and other spawn-taking facilities; the remaining 40 (or 23%) were from other sources (Table I). These returns were affected by sensory treatment. From releases of control and visually occluded fish, about 96% of the recoveries from sites other than Spring Creek (103 fish out of 107) were from spawn taking. Of the fish released with olfactory occlusion, 61% of the recoveries (28 out of 46) were from spawn-taking activities. Fish that had both senses occluded yielded rates of recovery lower than other groups, and 95% of the recoveries (18 out of 19) were from activities other than spawn taking.

Tagged fish recovered from all spawn-taking sites were usually trapped upon entry. Thus since fish could not leave, recoveries from sites other than Spring Creek were not necessarily a measure of straying but may reflect as well the amount of fish cultural activity in the area of the experiment.

Of the 132 recoveries from spawn-taking sites other than Spring Creek, 121 were within 24 km upstream from Bonneville Dam. Of the 121, 96 were from two hatcheries — Oxbow Hatchery, about 3 km upstream from the release site at Cascade Locks; and Cascade Hatchery, about the same distance downstream from that site. Of the tags recovered from Oxbow Hatchery, 93% were from control and blinded groups. Only 35% of the recoveries at Cascade Hatchery were control and blinded fish; 65% were fish with olfactory occlusions. These two hatcheries accounted for nearly all of the 28 fish with olfactory occlusion recovered from spawn-taking sites other than Spring Creek;

4 were recovered at Oxbow, and 22 at Cascade Hatchery. The remaining 2 were from Kalama Hatchery, about 144 km downstream from Bonneville Dam.

The orienting role of olfaction also was indicated when the fish chose spawn-taking sites other than Spring Creek. When the olfactory organs were blocked, fish were less likely to appear at such places. The only exception was at Cascade Hatchery where a number of fish with olfactory occlusions were recovered. The reason is unknown.

EFFECTS OF TIME OF RELEASE AND SIZE OF FISH ON RECOVERY

Recovery of the untreated control fish was affected by the time of release in the 18-day experiment and by the size of the fish (Fig. 3). From early releases of the controls, most recoveries were from Spring Creek, but the percentages recovered from later releases declined at Spring Creek and increased elsewhere. This change of behavior accompanied increased sexual maturity of fish released later and suggested that specific homing by olfaction may be masked during final stages of maturation — perhaps by the spawning drive itself — and that olfaction then may enable the fish to detect and seek other places where maturing fish are present.

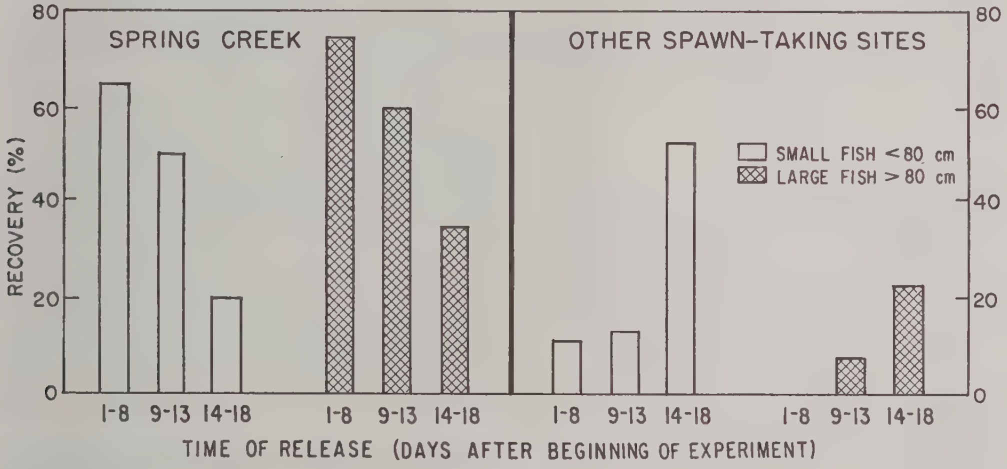

FIG. 3. Recoveries of control fish in two size-ranges at Spring Creek and other spawn-taking sites according to time of release.

Size of the control fish ranged from 55 to 106 cm (fork length). Most control fish that were recovered from spawn-taking sites other than Spring Creek were shorter than 80 cm. Although small fish were recovered at Spring Creek and elsewhere from all releases, most recoveries of the small fish released in the last 5 days were from sites other than Spring Creek. On the other hand, of control fish larger than 80 cm released throughout the experiment, the percentage of recovery was consistently higher at Spring Creek than at other sites; most recoveries of larger fish released in the last 5 days were still made at Spring Creek.

CONCLUSIONS

Olfaction appeared to be the major sensory mechanism directing the final migratory movements of chinook salmon in the Columbia River.

Olfactory occlusion reduced the return of the displaced fish to Spring Creek by a factor of over 10; this reduction indicated the primary role of olfaction in directing return of salmon to the hatchery. Olfactory occlusion also reduced the numbers of fish that arrived at most spawn-taking sites other than Spring Creek; olfaction probably also played a primary role in guiding fish to alternate sites.

Blinding reduced the return of the fish by a factor of 2; vision seemed to have a contributory but less essential role in the return. Blinding alone did not reduce the recovery of fish at spawn-taking sites other than Spring Creek.

Occlusion of both olfaction and vision reduced the recovery from all sources.

Recovery of control fish from sites other than Spring Creek increased with advancing sexual maturity and was more evident in small fish (less than 80 cm, fork length) than in large fish.

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Haliotis pourtalesii DALL, 1881 from Florida Waters

BY

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(Plate 18)

THE RARE ABALONE, *Haliotis pourtalesii* DALL, 1881, previously has been collected in the Gulf of Mexico on the steep continental slope bordering the Yucatan and Florida Straits (FOSTER, 1946; HARRY, 1966). Also, PARKER (1960) illustrated a fragmented shell of *H. pourtalesii* taken from a calcareous bank in the northwestern Gulf.

On April 21, 1967, personnel of the U. S. Fish and Wildlife Service, Bureau of Commercial Fisheries dredged a specimen from 45 fathoms on the continental shelf of Florida at Latitude 24°56.8′ N, Longitude 83°40′ W. The specimen was taken about 100 nautical miles west-northwest of the location reported by FOSTER (1946) and 20 fathoms shallower than any previous record. Although about 200 bottom grabs were taken along 8 transects from 5 to 1 800 fathoms between St. Petersburg and Key West, Florida, *Haliotis pourtalesii* occurred in only one sample.

The specimen is illustrated in Plate 18. Shell dimensions are: Height, 8 mm; maximum diameter, 30 mm; and minimum diameter, 21 mm. There are 28 pore tubercles, 6 of which are open. The color of the shell is brick red, with irregular splotches of tan scattered between the line of pores and the columellar border. The apex has a well-defined protoconch, pore tubercles, spiral and shoulder threads.

The specimen is deposited in the museum of the Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas. Identification was verified by Dr. Harold Harry, Texas A&M University.

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Explanation of Plate 18

Dorsal View of *Haliotis pourtalesii* DALL, 1881

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[1] Contribution No. 268, Bureau of Commercial Fisheries, Biological Laboratory, Galveston, Texas.

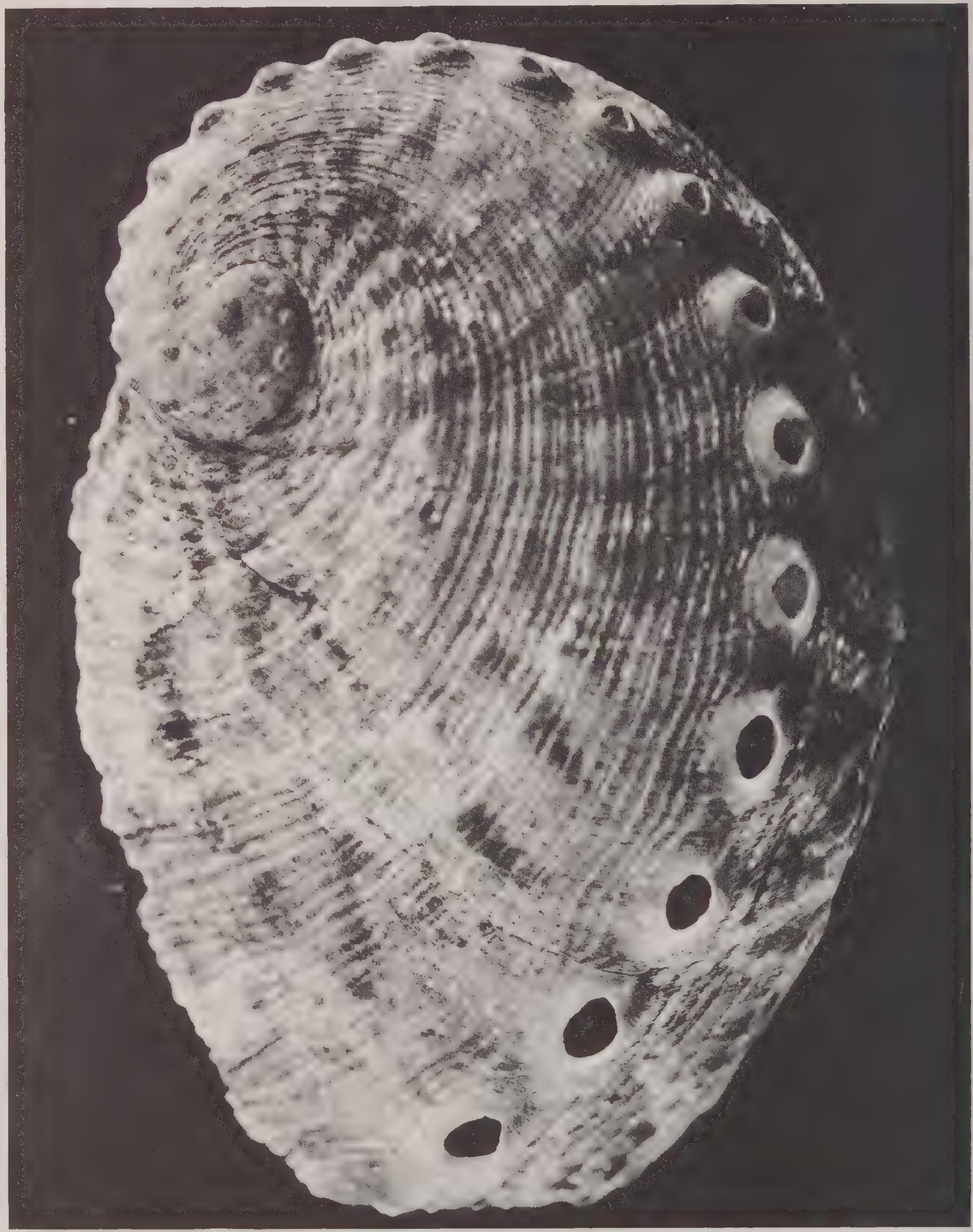

Figure 1

Chesapeake Science Vol. 9, No. 3, p. 163–172 September, 1968

Benthic Community Formation in a "New" Marine Environment

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ABSTRACT: Sequence of invasion of estuarine benthic organisms into a man-made pond was followed over a 2-year period. Dominant animals established early and developed a *Mya- Macoma- Nereis* association similar to that in nearby estuarine waters. Estimated biomass, faunal abundance, and growth measurements indicate that the benthic populations were near maximum levels within the first year, and that a stable association continued through the second year. Control of benthic populations will be essential if maximum production from selected food organisms is to be realized in artificial ponds.

Introduction

Opportunities to observe initial establishment of aquatic invertebrate associations are rarely presented to the ecologist. Most studies have followed the sequence of succession, or seasonal progression, for fouling organisms on newly constructed jetties, pilings, or floats, and on test plates exposed for selected time intervals. Reish (1961, 1963, 1964a, b, c) reviewed previous reports on this subject. The studies of Brandt (1897) and Reish (1956, 1961) followed faunal succession after dredging. Obviously, it is difficult to assess the effects of adult animals carried into the new area and to measure the volumes of water circulated.

In 1964, construction of four, man-made, salt-water ponds (Fig. 1) was completed at our laboratory site. Materials for the pond were carefully chosen to exclude the introduction of aquatic life. All water was supplied by pumps so that water volumes could be measured. The facility provided a unique opportunity to observe the sequence of invasion by marine invertebrates, particularly the infaunal organisms that could only enter during planktonic larval periods. A 2-year study was planned to follow this natural invasion. From earlier observations in newly dredged areas the specified time period was judged adequate for stabilization of any faunal association that might develop. In addition to the fundamental information that could be acquired about faunal establishment, the results would be valuable in determining whether control of natural populations would be necessary, or desirable, in future use of the ponds for research. This report describes continuous observations on the faunal colonization of one pond over 2 years and evaluates the consequences of natural populations on introduced species.

Pond Construction and Study Methods

Morphometric and construction features of the pond are shown in Fig. 2. Each pond is about ¼ acre in surface area (about 75 ft × 145 ft) and 3.3 ft (1 m) deep. A flexible polyethylene-sheet (6 mil) liner, buried about 10 inches under the sediments, makes the pond watertight. Water is supplied through 2-inch polyvinyl chloride (PVC) pipes by high-capacity pumps (360 gal/min), so that each pond could receive a maximum flow of 90 gal/min. Actually this volume was never achieved, since friction losses and other demands supplied by the same pump system reduced flow per pond to about 50 gal/min. The pond contains approximately 312,500 gallons of water. At the nominal flow rate of 50 gal/min, about 4½ days are required to replace

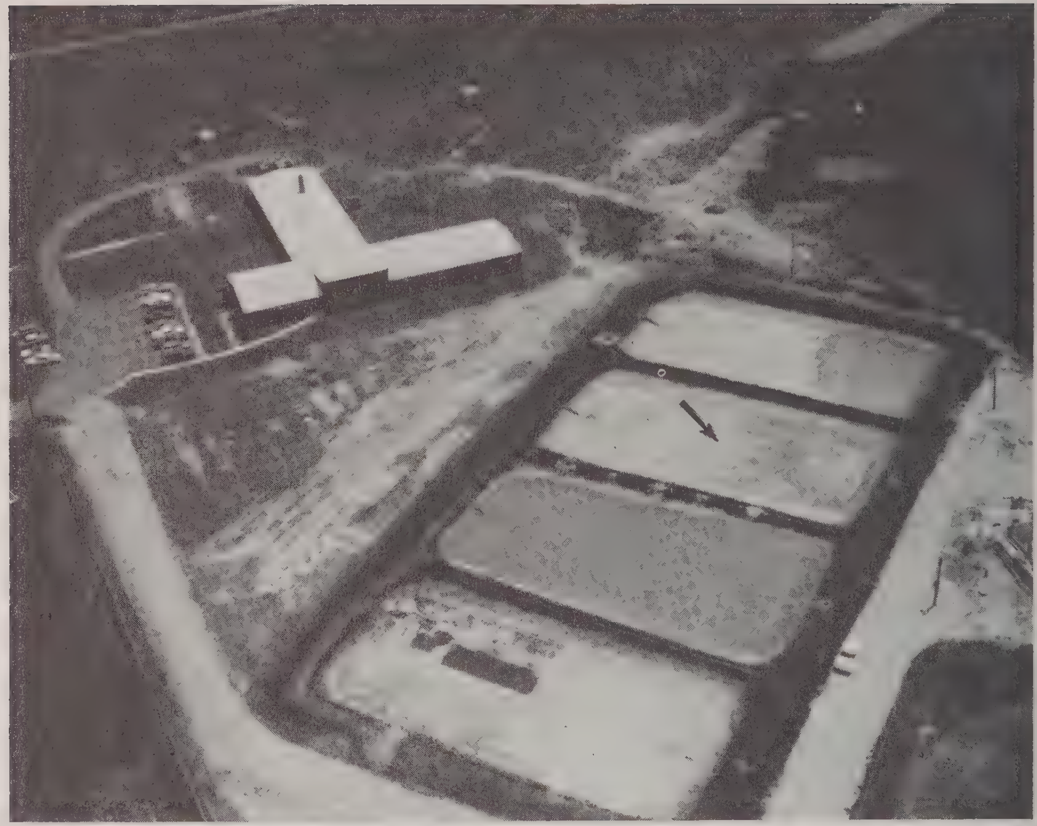

Fig. 1. Aerial view of the four man-made, salt-water ponds and the U. S. Bureau of Commercial Fisheries Biological Laboratory at Oxford, Maryland. Arrow indicates the pond used in this study and part of the distribution of sediment samplers.

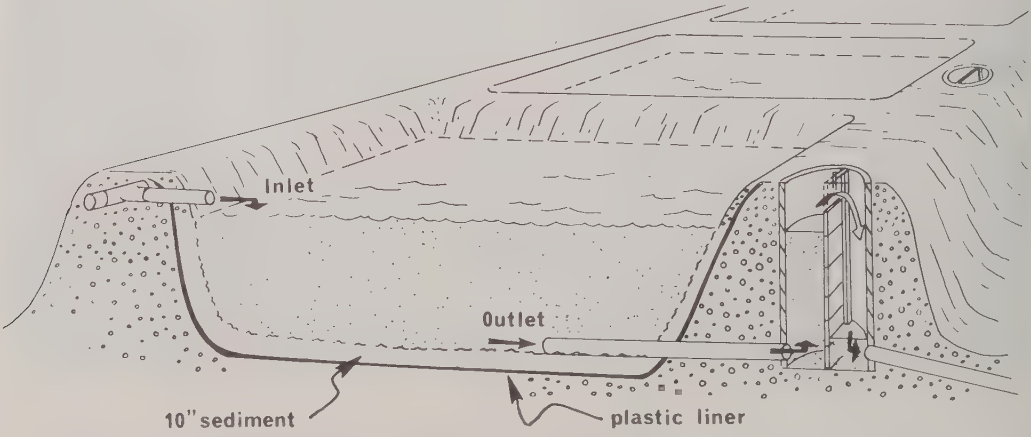
Inlet
Outlet
10" sediment
plastic liner

Fig. 2. Construction features of artificial salt water ponds.

the pond water, assuming the unattainable ideal of complete displacement and no mixing. Currents in the Tred Avon estuary have been observed at a maximum of 45 ft/min, and the average discharge has been estimated at 45 ft^3/sec. The pond would appear to have far less flow, or exchange, than the theoretical flow in the estuary. Actually, flow volumes in most areas of the estuary are considerably less than maximum and may be analogous to pond flow. A dual pipe system provides for periodic alteration of pumps and helps to prevent fouling. Water supplied at one end of the pond (inlet) circulates and flows through a drain and cistern at the other end of the pond (outlet). Water depth is controlled by the height of baffle boards in the cistern. A recording thermograph monitors water temperature and an aeration system provides saturation with dissolved oxygen and prevents formation of thick ice.

Data on temperature, salinity, and chlorophyll *a* for the 2-year period of this study are plotted in Fig. 3. Occasional determinations of dissolved oxygen (Winkler method) indicated that the pond was always at 100% saturation. Temperatures in the pond were generally slightly higher (about 1C) than in the adjacent natural water, perhaps because of the shallow depth and thorough insolation. Salinity was uniform and similar to concentrations in natural waters. Chlorophyll *a* was generally low, but appeared to be higher near the inlet than near the outlet. Perhaps this difference is due to removal by primary consumers in the pond population, but other factors could be accountable and may be defined by future studies. Generally, the ponds showed good circulation and thorough mixing and were without indication of vertical or horizontal separation in physical or chemical features.

Sediment samples of about 0.2 liter (i.e., the contents of a faunal sampler) were obtained at frequent intervals to follow changes in grain size distribution. Each sample was dried for 24 hours at 100C, gently ground with a mortar and pestle, and a subsample of about 100 g was passed through a standard screen series. Material retained by each screen was weighed and the percentage of each fraction calculated. The percentage of silt-clay in sediments near the outlet gradually increased during the 2 years (Fig. 4); sediments near the inlet maintained about the same relative composition. This observation might indicate that flow rates are somewhat slower near the outlet and that most sediment deposition occurs in this region of the pond. Sediment changes may also reflect different behavior of benthic species, or differences in the intensity of activity in relation to faunal abundance.

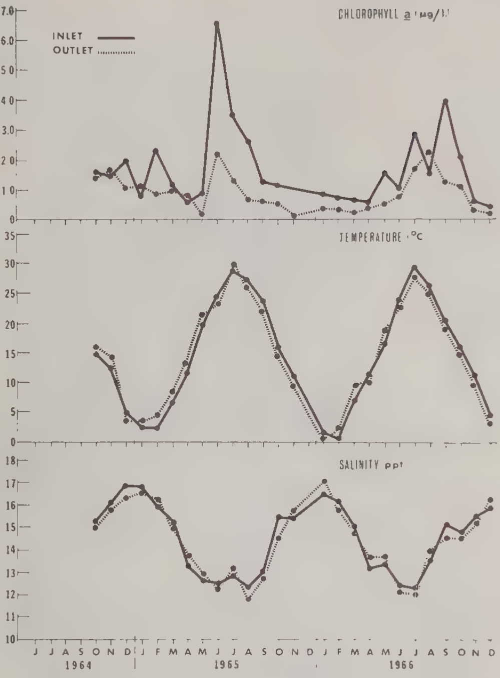

Fig. 3. Average monthly temperatures, salinities, and chlorophyll *a* concentrations for pond waters during the study.

The pond was, therefore, an enclosed, highly accessible body of water with environmental characteristics similar in many aspects to the nearby natural estuarine waters of the Tred Avon River and other regions of Chesapeake Bay (Hanks, 1964).

Before the first introduction of water in October 1964, about 175 sediment samplers were buried in the pond bottom on a regular grid pattern, and filled with pond sediment. The sampler was constructed

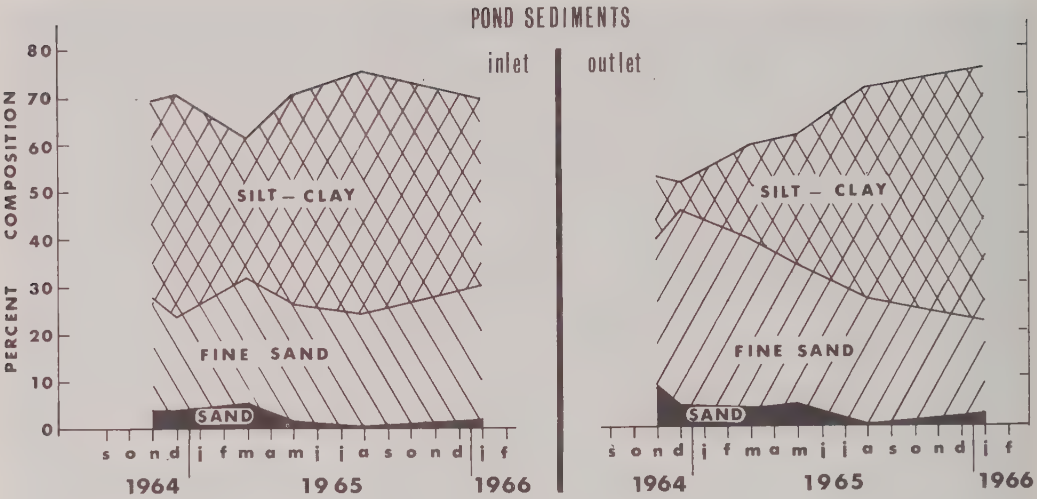

Fig. 4. Sediment composition from samples taken near the pond inlet (left) and outlet (right).

from the lower half of a 1-gallon polyethylene bottle, perforated on the bottom for free movement of water, and provided with a nylon becket and float for ease of retrieval. Each sampler enclosed an area of about 183 cm^2 and a volume of about 0.2 liter. Samplers provided an evenly dispersed sample pattern of known area and volume without the use of sampling instruments (grabs, dredges, . . .) that could damage the pond liner.

Each month, two samplers were removed from the bottom; one near the inlet, and one near the outlet. No special pattern of recovery was specified to obtain a random selection of samples. Contents of each sampler were passed through a set of screens in which the finest openings were 1 mm square. All organisms were identified and counted immediately. Occasionally, total lengths of dominant species were measured to obtain an indication of growth.

Results

Invasion Sequence of Species

First animals to enter the pond, as indicated by the first sample taken in November 1964, were small nektonic amphipods and polychaetes carried through the pumping system (Table 1). By the second month of exposure, two animals that eventually dominated the pond community, *Mya arenaria* and *Nereis succinea*, had established themselves in the pond sediments (Fig. 5). After an initial increase in population, *Mya* declined from a peak in the first spring, reached a low point during the second winter, recovered strongly in the second spring, and finally showed another decline toward the end of the observation period. The polychaete, *Nereis succinea*, maintained a steady and fairly low abundance for the first 9 months. Following spawning in May, the population gathered recruits and expanded to greater abundance through the final year.

Macoma balthica, a typical small bivalve of the bay, did not appear in pond samples for the first 6 months (November 1964 to April 1965), then rapidly increased to a level that was maintained throughout the remainder of the experiment. The closely related *Macoma phenax*, also a common inhabitant of the bay, did not appear until July 1965 and never attained appreciable numbers.

Other animals showing fairly consistent abundance were the amphipods *Carinogammarus mucronatus* and *Cymadusa compta*. Both organisms are so highly motile that little significance can be attached to their numbers from bottom samples. Indeed, since they are extremely wide-

Table 1: List of species and frequency of occurrence from monthly samples. No samples were taken in Feb. and Oct. 1965, and July 1966.

Species	1964 Nov.		Dec.		1965 Jan.		Mar.		Apr.		May		June		July		Aug.		Sept.		Nov.		Dec.		1966 Jan.		Feb.		Mar.		Apr.		May		June		Aug.		Total
	*I	O	I	O	I	O	I	O	I	O	I	O	I	O	I	O	I	O	I	O	I	O	I	O	I	O	I	O	I	O	I	O	I	O	I	O	I	O	
Mya arenaria			6		22	5	5	1	20	3	36	14	15	9	34	5	28	4	19	11	4	1	5	3		2	12	3	14	4		7	40	2	1			10	345
Nereis succinea			7	3	2			2	2	3	7	6	2	3	1	2	7	5	10	5	14	9	7	16	17	9	12	11	10	12	8	7	9	8	10	10		12	248
Macoma balthica									3			5	7	9				8	8	8	8	7	6	10	12	12	6	5	4	8	10	5	6	17	18	1		27	210
Carinogammarus mucronatus	3	4	3	4			8	9	3	7			20	3			2								1										26	2			95
Cymadusa compta	2		12	4	2	20	6	12		4	1	3	2	1				4	2		2	2			2	2													83
Polydora ligni	1				20	4	17	6	6		4	7																											65
Macoma phenax															9	4			1			4	11	3				1	2	1	6	2	2					2	48
Molgula sp.			1	6							1	5	2	3								1																	19
Eteone heteropoda			2			1	2	2	4																														11
Chironomid larva						1			2	3			1	1	3																								11
Polydora ciliata			5	4																																			9
Rhithropanopeus harrisi																									1													7	8
Nemertea sp.					1			2				1	2									1																	7
Maldanid																													4										4
Odostomia bisuturalis					2																																		2
Pectinaria gouldi																			1						1														2
Brachiodontes recurvis																																	2						2
Elysia chlorotica			1												1																								2
Asabellides oculata																	1																						1
Odostomia trifida																	1																						1
Mulinia lateralis																								1															1
Erichsonella attenuata																									1														1
Total	6	4	37	221	449	331	38	34	40	20	49	41	51	29	48	11	39	21	41	24	28	25	29	33	34	26	30	20	34	25	24	23	57	27	55	13	0	58	1175
Mean	5		29		40		36		30		45		40		30		30		33		27		31		30		25		30		24		42		34				

* I = Inlet side of pond; O = Outlet side of pond.

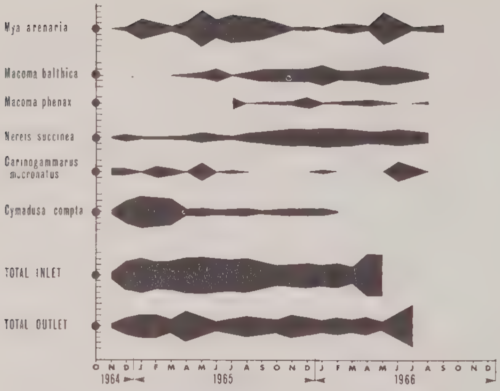

Fig. 5. Occurrences and abundance of some predominant species in a man-made, salt-water pond. The lowest two diagrams are only one half the scale of the others and show the total fluctuations in abundance between pond inlet (upper diagram) and pond outlet (lower diagram).

spread in the natural estuary, near the intake to the water supply system, they could easily be transient adults passing through the pond with the water.

One species that played an important role in the faunal association but whose abundance was not accurately estimated from the benthic samples, was the mud crab, *Rhithropanopeus harrisi.* When an adjacent pond was drained after a period of 10 months, the mud crab population was estimated at over 30,000, an average of 3/ft^2. Predatory activity of the mud crab was undoubtedly the major controlling factor for the *Mya* population.

Factors that influenced faunal composition of the pond are varied. Species composition in the pond is determined by the endemic species of the estuarine water source. From qualitative and quantitative surveys in the Tred Avon River, I have found about 50 species of benthic organisms. Of these, only 10 are prominent species in the soft mud and sand bottoms near the laboratory:

Bivalves

Gemma gemma
Mulinia lateralis
Mya arenaria
Macoma balthica
Macoma phenax

Snails

Retusa canaliculata
Odostomia trifida
Hydrobia minuta

Worms

Nereis succinea
Scoloplos fragilis

Factors limiting access of these species are method of reproduction and length of larval or pelagic existence. An excellent example of the control of dispersion by reproductive processes is the little gem clam, *Gemma gemma. Gemma* is ovoviviparous, using the demibranchs as brood pouches. No planktonic stage is evident and the juveniles are released as brood pouches. Dispersion is accomplished by crawling with the foot and washing by water currents along the bottom (Selmer, 1967). *Gemma* would rarely be found 3 or 4 feet above the bottom at the level of the intake for the pond's water supply. Therefore, even though *Gemma* is in great abundance near the laboratory, it did not establish in the pond.

Mulinia lateralis is another prominent bivalve in local waters that did not establish in the pond; only one specimen was found in the 2-year study. *Mulinia* spawns from May to November in the Tred Avon River (Shaw, 1965) and larvae would have been available during most of the critical early period of faunal invasion; however, peak setting generally occurs in September. Apparently, some other factor works against the establishment of *Mulinia;* the most likely choice would be sediment composition although no direct evidence is available. *Mulinia* and *Gemma* are the two most notable species missing from the pond, but plentiful in the river. Nearly all other predominant organisms did establish in the pond, although some in minor numbers.

The Pond Association

Species density was notably higher near the pond inlet than near the outlet (Fig. 5). Several factors may be implicated in this differential abundance. Larvae may be stimulated to set by the physical disturbances created in passing through the pumping system. For those species that are gregarious, immediate settling by a few individuals near the inlet will make this area more attractive to larvae that enter the pond later. Additionally, survival of juveniles, and perhaps larvae, may be limited by lack of food materials, which have been removed from the water by organisms closer to the inlet. By the end of the first year of pond exposure, the "climax" association of *Mya arenaria, Macoma balthica,* and *Nereis succinea* was thoroughly established. These three species characterize one of the major communities of the Tred Avon River; they established early in the pond, and maintained dominance thereafter. Although the pond populations of the three species did fluctuate in the second year, relative abundance did not change. Indeed, periodic observations in 1967, after termination of faunal sampling, showed that the association continued to maintain the predominant three-species association. Epifaunal animals, not the primary interest of this study, showed greater fluctuations, and highly motile organisms (crustaceans, fish, . . .) were most variable in abundance.

Predation was possibly the most critical factor in controlling abundance of *Mya* in the pond. The mud crab, *Rhithropanopeus harrisi,* a common inhabitant of our local estuarine waters, generally releases larvae in early to mid-summer. These larvae would not be available to enter the pond in the fall and winter of 1964, but in 1965 recruitment of mud crabs must have been especially successful. By the fall of 1965, abundance of soft-shell clams had declined noticeably, and broken clam shells were evident in nearly all samples. Predation was clearly centered on the larger sizes of clams, and *Mya* apparently was preferred over either species of *Macoma.* Population estimates in 1966 showed that clam recruitment was adequate to rebuild the *Mya* population, but predation again decimated the population by late fall. Apparently this cyclic fluctuation will continue.

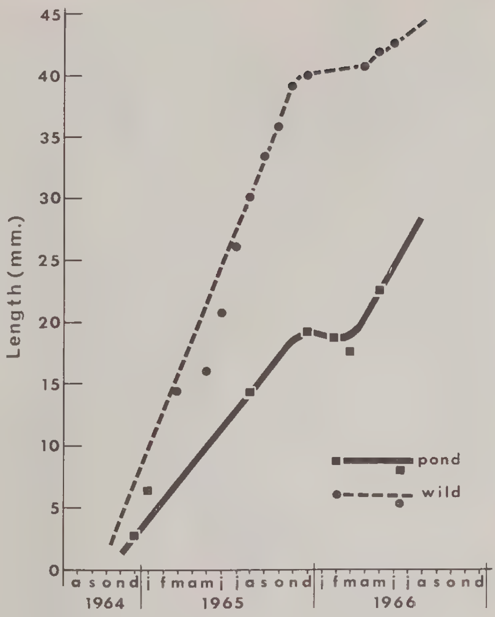

Fig. 6. Growth of *Mya arenaria* from captive and natural populations of the Tred Avon River (dashed line) and pond populations (solid line).

Intraspecies competition was most evident in the *Mya* population. Growth was slower (Fig. 6) in the pond clams than in captive and wild populations in the Tred Avon River.[1] At densities above 100 clams/ft² during some periods of the pond study, the competition for food materials was intense. Chlorophyll *a* analyses (which indicate phytoplankton abundance) showed that chlorophyll declined near the bottom and with increasing distance from the inlet. Apparently, filter-feeding activity was sufficient to deplete the food supply and hence to slow the growth of *Mya.* Maintenance of "natural" growth rates by *Macoma balthica* and *M. phenax* (Fig. 7) reflects their feeding methods and behavior. Whereas *Mya* is a filter-feeder using water near the sediment interface, *Macoma* lives close to the surface of mud sediment (Brady, 1932; Frazer, 1932; Thamdrup, 1935), and is a deposit feeder. The inhalant siphon sweeps in a circle around the animal sucking up mud and detritus with the contained organisms.

Macoma populations were evenly dis-

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[1] Information on captive and wild populations obtained from unpublished growth data on file at the Bureau of Commercial Fisheries Laboratory, Oxford, Md.

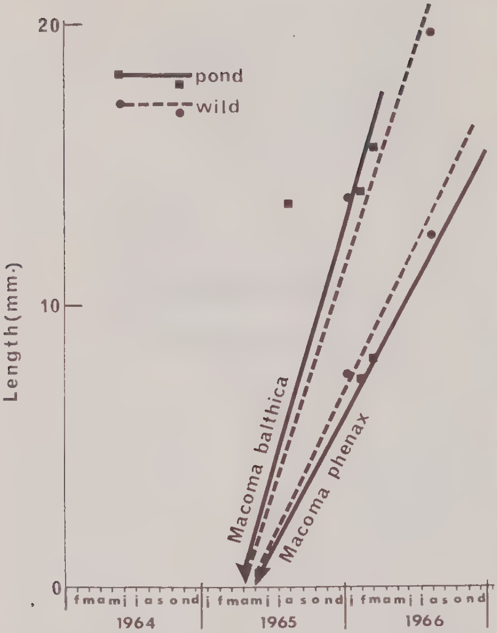

Fig. 7. Growth of *Macoma balthica* and *M. phenax* from natural populations of the Tred Avon River (dashed lines) and pond populations (solid lines). The origin of the growth lines is taken as the approximate period of peak spawning in natural waters. Points for natural populations are average size at first winter check (first point) and average total length at collection (second point). Points for pond populations are based on average total length at each collection period.

tributed in the pond and no consistent concentrations were observed in either end. Dexter (1947) has shown that in mixed *Mya-Macoma* communities, the abundance of one species is inversely proportional to the other. *Macoma* is apparently more mobile than *Mya*, perhaps in response to the necessity of seeking new surface areas when the local supply of food material is exhausted (Yonge, 1949; Bradfield and Newell, 1961). Even though *Mya* and *Macoma* may metamorphose and set under the same environmental stimuli, thereby having similar initial distributions, the mobility of *Macoma* is retained in the adult stages, whereas the active movement of *Mya* is restricted to the juveniles and the clam depends upon currents and tidal action for re-distribution (Smith, 1952).

The polychaete *Nereis succinea* was the second most abundant animal in the pond community. In the mid-Chesapeake Bay region, *N. succinea* develops a heteronereis form and spawns in early to mid-May. The simultaneous spawning activity literally fills the water with sexually mature worms and the annelids are known locally as "May-worms." Larvae are found in the water during the next 2 to 4 months, but the peak of larval abundance is usually passed in the first 3 weeks. Although some *N. succinea* were found early in the pond study, the major period of recruitment occurred in the summer of 1965. Regular observations indicated that growth of worms in the pond was similar to that of worms living in the natural waters nearby. Nereids in the pond were found crawling freely on the sediment surface, as well as in typical U-shaped burrows. *N. succinea* populations were slow to build up, but once established were fairly stable. In the summers of 1966 and 1967, *N. succinea* heteronereids and spawning were observed in the pond about 2 weeks after the peak of spawning in the river. Temperatures at the spawning peak were 14.5 C in the river and 16 C in the pond.

Nereids have been generally classed as carnivorous, but are now known to feed by various methods on a wide variety of food materials. *Nereis diversicolor*, a typical estuarine animal, is a consumer of detritus (Rauchenplat, 1901); it was described by Blegvad (1914) as a herbivorous detritus eater which may also be carnivorous. Thamdrup (1935) thought this species to be both a selective and a non-selective feeder. Nereids are also reported to be filter feeders that use a secreted-mucus feeding funnel (Harley, 1950; Wells and Dales, 1951). Amos (1957) indicated that *Nereis succinea* fed in diverse ways since stomach contents included obvious prey animals as well as detritus, algae, diatoms, and sediments. Sanders, et al. (1962) found that nereids in Barnstable Harbor, Mass., were omnivorous. Such diverse feeding habits allow for considerable adaptability to changing environmental conditions and food supply, and may account for uniform distribution within the pond.

As can be seen from Table 1, no other benthic species maintained comparable abundance levels throughout the study. Amphipod abundance fluctuated widely and, as indicated previously, they were possibly transients passing through the pond with the water masses. The sea squirt, *Molgula,* is a common fouling organism in this region, but specific requirements for firm substrate limits occurrence in the pond. *Polydora ligni,* a polychaete, was abundant early in 1965 near the pond inlet, but declined through the spring and was not found after May 1965.

ESTIMATES OF STANDING CROP IN THE POND

In the summer of 1967, wet weights of benthic species in the Tred Avon River were established from 0.1 m² Petersen grab samples. Size ranges for these animals were similar to those in pond populations. Methods of obtaining wet weights were those commonly used (Thorson, 1957); shells of mollusks were included in the weights. The mean wet weight of each species in the natural population was assumed to be a logical estimate of mean wet weight for the same species in the pond. There are obvious objections to this approach, but I believe that the derived estimates of pond biomass are reasonable and provide a basis to assess potential pond production.

The average wet weights per individual of the predominant pond organisms, as estimated from natural populations, are:

Mya arenaria	0.34 g
Macoma balthica	0.22 g
Macoma phenax	0.02 g
Nereis succinea	0.10 g
Rhithropanopeus harrisi	0.16 g

From the maximum species numbers of Table 1, the maximum calculated biomass of these predominant organisms is estimated at 1360 g/m². This figure represents the benthic organisms plus the mud crab population only; and total pond biomass is obviously much greater. The pond benthos is highly productive in comparison with figures cited for other regions. Ellis (1960) found that arctic *Macoma* communities produced standing crops of about 200 g/m², and Vibe (1939) reported crops ranging from 50 g/m² to 1500 g/m² in warmer waters. Spärck (1935), who summarized the results of numerous studies, showed that the average weight of living animals per square meter ranged from 6 to 350 g, and that in some shallow-water areas weights reached 700 g/m². From Thorson (1957) and Ellis (1960) it can be estimated that dry weights are about 10% of wet weights. Such a conversion applied to the pond biomass gives a figure of 136.0 g/m², which is 2 to 8 times the range of dry weights (17.6–60.2 g/m²) established by Sanders et al. (1962) for the rich intertidal mud flats of Barnstable Harbor, Mass., and more than 10 times the dry weight (12.29 g/m²) in Buzzards Bay (Sanders, 1960). Benthic populations in the pond are apparently near the upper level of maximum production and can be expected to offer vigorous competition for the limited food materials available.

NATURAL VS. SELECTED POPULATIONS

Man-made and natural ponds have been considered ideal systems for intensive cultivation of marine organisms. In many areas of the world today, particularly Asia, the cultivation of shrimp, small fish, and shellfish in ponds and lagoons has demonstrated that protein production can far exceed the best levels of terrestial areas. One group of animals that appear to be suited for pond cultivation are the bivalve mollusks, such as oysters, clams, and mussels.

This study has demonstrated that in ponds with constantly flowing water, benthic communities, prevalent in nearby areas, will quickly establish in the pond and that intensive competition can occur. These pond communities must be limited or excluded if the greatest organic production is to be centered in selected food species, particularly if the selected species are filter-feeding aquatic shellfish. Populations can possibly be restricted by chemical means similar to those commonly used in present-day agriculture, but biological and physical controls are also available. Clearly, small ponds supplied by natural waters from local estuarine tributaries would not be adequate to support large volumes of food organisms. To achieve maximum yields, competition from associated organisms must be eliminated, ponds must be fertilized, or other means devised to stimulate productivity. Previous knowledge of pond ecology is essential to selection of management methods and to the estimation of potential pond production.

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RELATION OF FECUNDITY AND EGG LENGTH TO CARAPACE LENGTH IN THE KING CRAB, *PARALITHODES CAMTSCHATICA*

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ABSTRACT

The fecundity of female king crabs, collected in Kachemak Bay, Alaska, in July, 1967, increased with carapace length, but egg length did not. For crabs of the same size, the mean number of eggs carried was significantly greater than for crabs in a similar study in Kachemak Bay in July, 1960.

INTRODUCTION

The U. S. Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska, has started a long-term study of the reproduction of the commercially important king crab, *Paralithodes camtschatica* (Tilesius), in Kachemak Bay off Cook Inlet, Alaska. Female king crabs spawn in early spring and carry the developing embryos on their pleopods for about one year. It is expected that during this time fecundity (the number of eggs or developing embryos) will decrease. Therefore, fecundity is being determined periodically during the year to measure this decrease. These data will be used to derive equations for estimating the average fecundity of the population at each sample date and to predict the probable number of larvae that would result.

Although many authors have reported on the number of eggs carried by the king crab, only Sato (1958), Bright, Durham, and Knudsen (1960) and Rodin[1] determined the number of eggs over the entire size range of ovigerous crabs. Sato based his studies on king crabs from the North Pacific Ocean off Nemuro, Japan; Rodin used king crabs from the Bering Sea; and Bright *et al.* did their research on king crabs collected in July in Kachemak Bay — the same area and time of year that I sampled.

In this report I describe the relation of fecundity and egg length to the carapace length of female king crabs collected July 14-25, 1967, in Kachemak Bay. These data are compared with the findings of Bright *et al.* (1960) to determine any changes in these relations in 1960 and 1967.

SAMPLE COLLECTION AND TREATMENT

Crabs were taken in pots similar to those used in the commercial king crab fishery. The pots were set 30 to 40 m deep and were usually checked every other day. Carapace lengths (posterior margin of the right eye socket to the mid-point of the posterior margin of the carapace) of ovigerous crabs were measured to the nearest 0.1 mm. To ensure representation of all sizes of ovigerous crabs, 90 were selected on the basis of their carapace length over a range of 98 to 175 mm. The egg masses, with the pleopods attached, were removed from the females by excising the pleopods at their base and placed in plastic bags.

The number of eggs in each mass was determined in the laboratory by sampling. Each egg mass was weighed (after blotting) to an accuracy of ±0.01g, and a sample of eggs (about 5 per cent of the total weight of each mass) was removed, weighed, and counted. The count-weight ratio was used to estimate the total number of eggs in the mass. For counting, the eggs in each sample were separated from the hairs of the pleopods by soaking the sample in a saturated solution of sea water and sodium hydroxide for about 24 hours, and then rinsed several times in 10 per cent formalin. Repeated counting of several samples indicated a counting error of 0.08 per cent.

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[1] Rodin, V. E. 1966. Soviet works of 1965 on the distribution of Kamchatka crab supply conditions *Paralithodes camtschatica* (Tilesius) in the southeastern part of the Bering Sea. (unpublished manuscript)

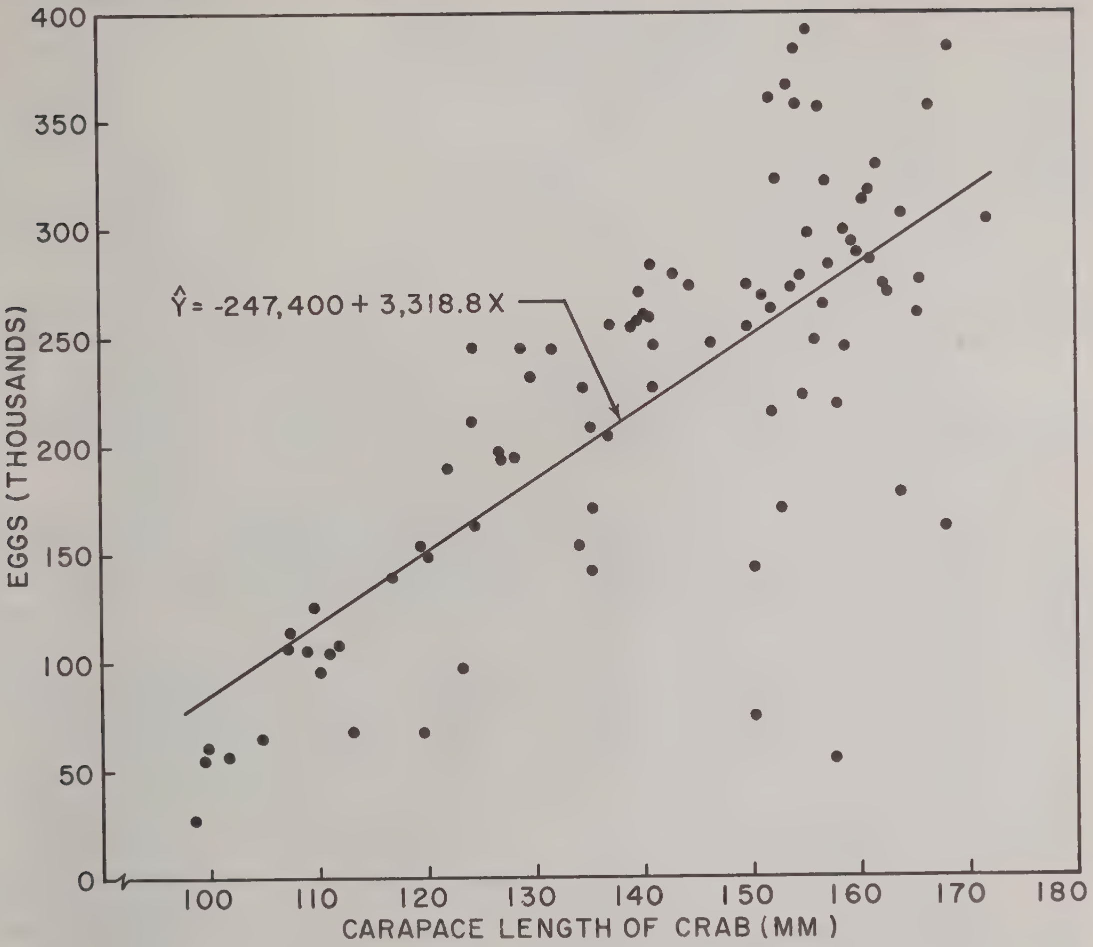

FIG. 1. *Estimates of fecundity of 90 king crabs collected in Kachemak Bay in July, 1967 and a computed linear regression of fecundity on carapace length.*

RELATION OF NUMBER AND SIZE OF EGGS TO CARAPACE LENGTH

In general, fecundity increased as carapace length increased. There was a wide range in the number of eggs carried by crabs of any given carapace length, and this range increased with carapace length (Fig. 1). The greatest range was in crabs whose carapace lengths were between 150 and 170 mm. Females in this size group had 25,000 to 390,000 eggs. To describe the relation of fecundity to carapace length, I computed a linear regression of fecundity (Y) on carapace length (X):

$$\hat{Y} = -247{,}400 + 3{,}318.8X$$

The cause of the wide range in fecundity is unknown, but it is possible that an exceptionally low number of eggs results when a female mates with a less than fully capable male. Powell and Nickerson (1965) found that, although a male king crab can mate successfully with at least five females, it may not be capable of fertilizing all the eggs of subsequent females. This inability may result in many unfertilized eggs, which do not adhere to the pleopod hairs. This possibility has an important bearing on the king crab fishery, because only males are harvested.

To compare my estimates of numbers of eggs with those of Bright *et al.* (1960), who presented their data as the mean number of eggs for each

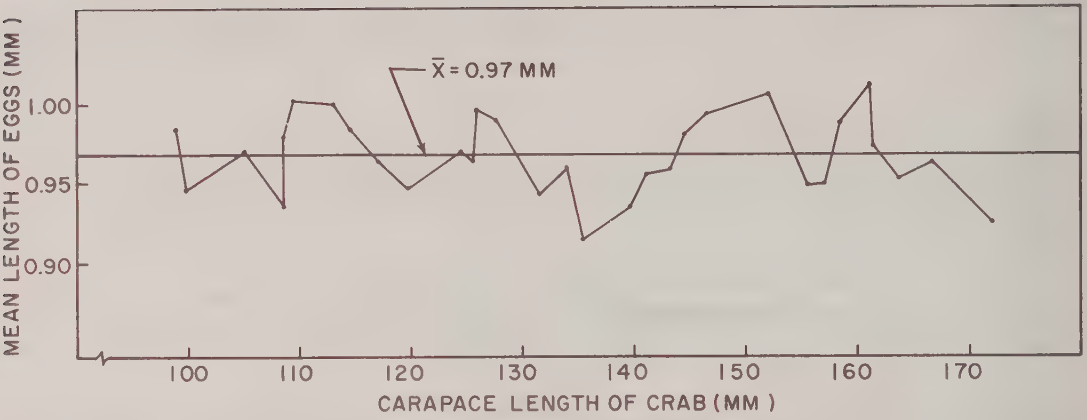

FIG. 2. *Relation of mean length of 50 eggs to carapace length for 31 female king crabs collected in Kachemak Bay in July, 1967.*

10-mm size class of crab, I computed a linear regression of the number of eggs (Y) on carapace length (X) for their data. Analysis of covariance was used to compare the regression coefficients and adjusted means of the two groups of data. At the 1-per cent level the regression coefficients were not significantly different (F = 5.336; 94 d.f.), but the adjusted mean number of eggs in my study was significantly greater — by about 11,000 eggs (F= 751.6; 95 d.f.) — than that calculated from the data of Bright *et al.* (1960).

The lengths of 50 unpreserved eggs from each of 31 crabs were measured (with an ocular micrometer) to determine if the size of the eggs increased with the size of the crab (Fig. 2). The mean egg lengths varied among the crabs but could not be related to carapace length. The mean length of 1,550 eggs measured in my study was 0.97 mm — almost the same as the mean of 0.98 mm calculated from measurements of 480 eggs by Bright *et al.* (1960).

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EXPLOITATION AND BIOLOGICAL RESEARCH OF ATLANTIC MENHADEN

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Abstract

Menhaden occur in the Continental Shelf waters from Nova Scotia, Canada, to Mexico and support the largest commercial fishery in the United States in terms of pounds landed. The peak catch of 2.3 billion pounds was in 1962. The method of feeding, the general life history, and the migrations of menhaden are briefly discussed. The efficiency and intensity of the commercial fishery have greatly increased in recent years, but the catch of Atlantic menhaden declined 64 percent between 1962 and 1967. Most of the biological research to date on these fish has been concerned with determining the biological characteristics of the stock as measured by the commercial catch. Data on age, size, sex ratio, and fishing effort are available since 1955 and will form the basis for management practices. Additional research on menhaden along the Continental Shelf is needed, particularly for determining periods critical to survival.

* * * * *

Menhaden (genus Brevoortia) are herringlike fishes that occur in the Continental Shelf waters from Nova Scotia, Canada, to Mexico. Two species, an Atlantic menhaden, ranging from Canada to the east coast of Florida, and a Gulf menhaden, ranging from the west coast of Florida to Texas, make up the bulk of the resource. Although this is a fish which you never see on the dinner table, menhaden support the largest commercial fishery in the United States, in terms of weight landed. In 1962, the peak year of production, the combined catch from the Atlantic and the Gulf of Mexico of 2.3 billion pounds amounted to 44 percent, by weight, of the total U.S. commercial catch of all species. The peak catch from the Atlantic fishery was 1.6 billion pounds in 1956.

Menhaden are small, oily fish closely related to the shad, alewife, herring, and sardine. Most of those caught are less than 12 inches long and weigh less than 1 pound.

Not only are menhaden of commercial importance, but they play an important and fundamental role in the waters over the Atlantic Continental Shelf. While feeding they swim through the water with their mouths gaping and filter small planktonic organisms through a very efficient and complex gill and pharyngeal apparatus. Thus, they subsist mainly on the primary production of the ocean and are themselves a source of food for many other species of fish.

Menhaden have a rather complex life history. Spawning and early egg and larval development occur in the water over the Continental Shelf or in high-salinity inshore waters; larvae

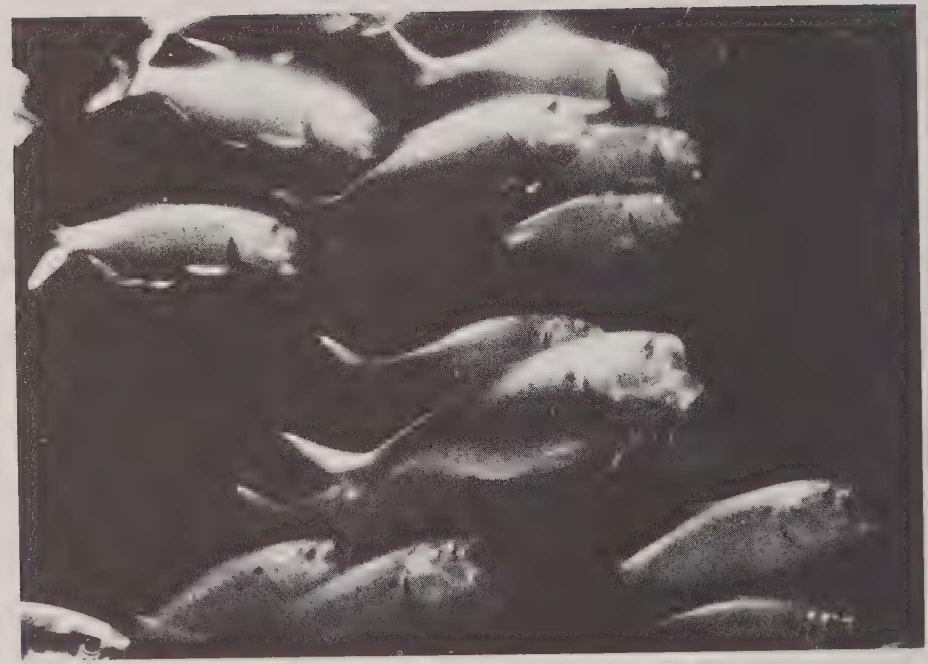

Figure 1.--School of Atlantic menhaden. Note gaping mouths and extended gill covers.

enter estuaries and proceed almost to fresh water; juveniles (fish less than 1 year old) return to more saline waters; and adults migrate extensively along the coast. Thus, these fish are exposed to a number of variable factors such as temperature, salinity, currents, pollution, and fishing, any of which could affect their ultimate survival.

Migrations of menhaden are extensive. They migrate seasonally along the Atlantic coast--northward in the spring and summer (going farther northward each year as they become older) and southward in the fall. These migrations reportedly depend on water temperatures over 50° F. The fall migration is composed of maturing fish moving south to spawn off North Carolina and other South Atlantic States. Although some spawning occurs off New York as well as along the Middle Atlantic Coast during the southward migration, the major spawning area is believed to be south of Cape Hatteras, N.C.

A commercial fishery for Atlantic menhaden has existed since colonial days, but it was not until purse seines were introduced in about 1850 that the fishery really started, and it was not fully developed until after World War II. The major Atlantic fishing areas are South Atlantic, from Florida to Cape Hatteras, N.C.; Chesapeake Bay; Middle Atlantic, from Chesapeake Bay to Long Island, N.Y.; and the North Atlantic, from Long Island northward.

Because menhaden move in large dense schools, purse seines have proved to be the most effective method of catching them. A menhaden purse seine is about 1,200 feet long and 60 to 90 feet deep, and is usually made from synthetic webbing. Two small purse boats circle the menhaden school in opposite directions, letting the net out to surround the fish. The bottom of the net is then drawn together, or pursed, to form a bag around the fish. The fish normally are then loaded aboard a larger carrier vessel by means of a suction hose and hydraulic fish pumps.

The catch from a single set of the purse seine may vary from only a few thousand fish for a poor set to several hundred thousand for a good set. The average catch per set in recent years has been between 60,000 and 75,000 fish.

On the Atlantic Coast, fishing is normally a 1-day operation; the boats leave early in the morning and return to the fish plants the same day. Fishing takes place in the daytime, usually in relatively shallow inshore waters.

The efficiency of the fishing operations has been greatly increased in recent years through the use of improved gear and methods. The newer carrier vessels are larger and faster, permitting them to fish farther from the plant. The use of airplanes to scout for menhaden schools has greatly increased the area that can be covered. Other innovations are power blocks for hauling in the net more easily and faster; lighter synthetic webbing (which permits larger nets to be used); and suction

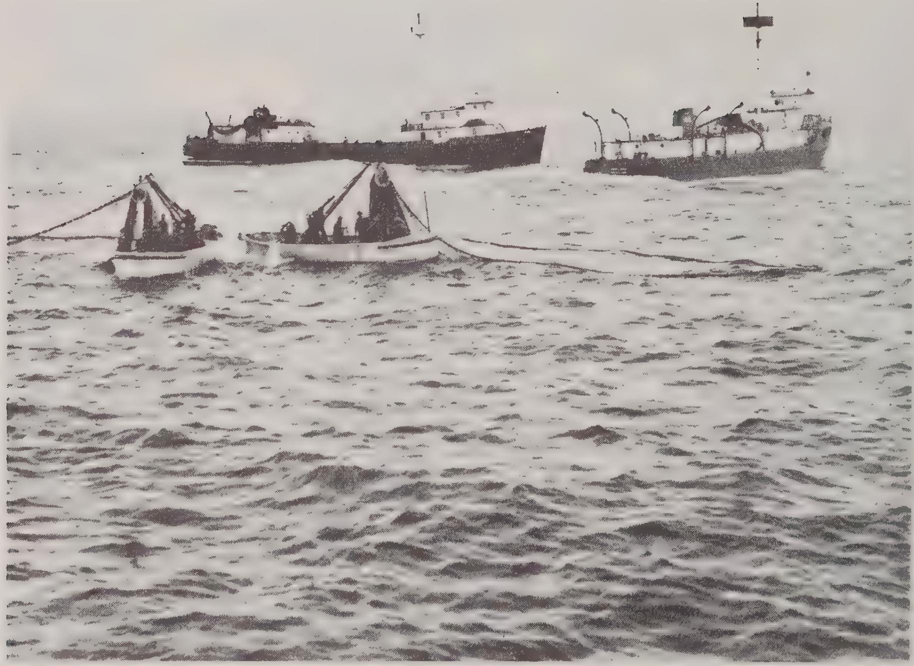

Figure 2.--Bringing in a menhaden purse seine through power blocks in the purse boats. Two larger carrier vessels in the background.

hoses for faster unloading of fish from the net. As a result of these improvements, the menhaden fishery is now one of the most progressive fisheries in the United States and in recent years it has been the most intensive in its history.

All menhaden caught go into the manufacture of fish meal and oil. Rich in protein, menhaden meal makes an excellent food supplement for poultry, hogs, mink, and other animals. The oil is used in a variety of products, including paints, soaps, and lubricants. Here is a single domestic fishery resource that is capable of annually supplying as much high quality protein as the combined landings of most of our other major domestic fisheries such as salmon, tuna, shrimp, and crabs.

The abundance of menhaden fluctuates greatly, apparently because of variations in the survival of individual yearly spawnings (year classes). During the 10-year period 1955-64, the most successful spawning (1958) yielded about seven times as many fish to the fishery as the poorest year class (1964).

In addition to annual fluctuations in abundance, the Atlantic menhaden stock has undergone a drastic, continued decline in abundance in the past 5 years.

Table 1.--Landings of Atlantic menhaden caught in the purse seine fishery, 1940-67

Year	Thousands of tons	Year	Thousands of tons	Year	Thousands of tons
1940	221.5	1950	327.5	1960	584.0
1941	306.5	1951	398.5	1961	635.0
1942	184.5	1952	452.0	1962	593.5
1943	261.5	1953	654.0	1963	381.5
1944	284.5	1954	670.0	1964	299.5
1945	326.5	1955	707.5	1965	301.5
1946	399.5	1956	785.0	1966	242.0
1947	417.0	1957	668.5	1967	213.5
1948	382.0	1958	562.5		
1949	401.0	1959	726.5		

The 1967 Atlantic catch was down 64 percent from that of 1962. This decline is due principally to poor survival of all year classes since 1958, compounded by a very intense fishery on the younger fish. To harvest the very abundant 1958 year class, the industry significantly increased fishing effort in the early 1960's. Then, after several consecutive years of poor survival, three things happened: (1) too few fish were available to support the large fishing fleet, and the catch per unit of fishing effort dropped significantly; (2) in an attempt to maintain the catches, a greater and greater proportion of the younger, immature fish were caught, principally in Chesapeake

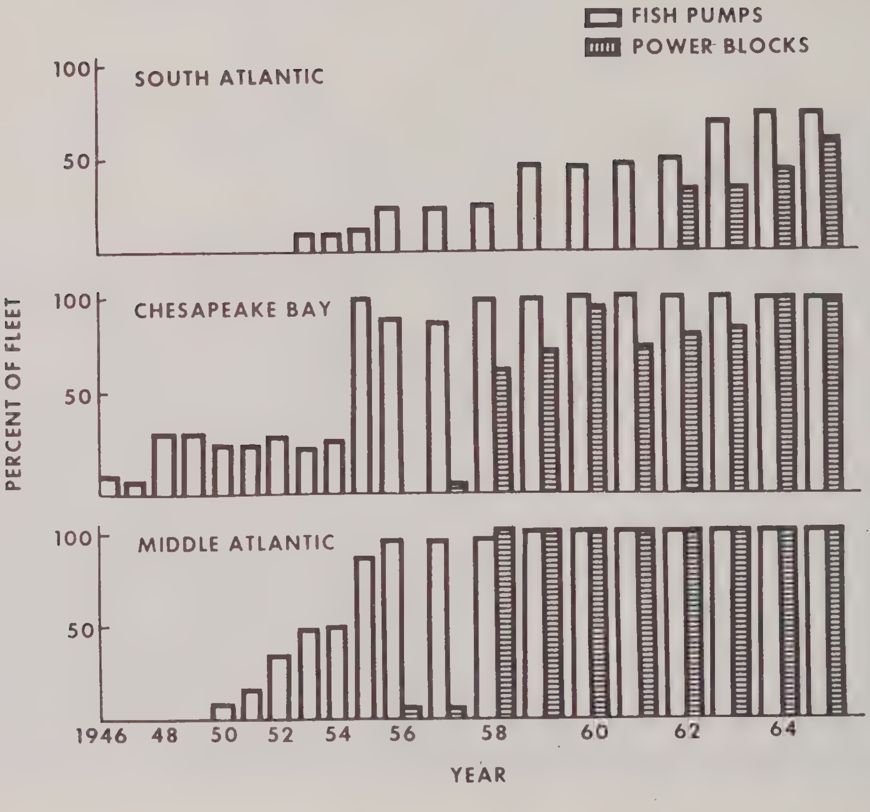

Figure 3.--Percent of the Atlantic menhaden fishing fleet using fish pumps and power blocks in three major fishing areas, 1946-65.

Bay; and (3) the older fish disappeared from the stocks and this loss eliminated the fishery off New England and caused a considerable reduction in both the abundance of menhaden and fishing effort off the New York and New Jersey coasts. It is apparent that for a resource such as menhaden, which experiences wide fluctuations in abundance, the classical concept of a fixed maximum sustained yield will not apply. Instead, the amount of fishing effort and the optimum catch must be periodically adjusted according to the abundance of the resource.

Because of the wide distribution of menhaden, biological research on this resource by individual states would have limited application. Consequently, the major research responsibility has been vested in the U.S. Bureau of Commercial Fisheries through our laboratory at Beaufort, N.C. This research program was started in 1955 and is aimed principally at determining the level or levels of utilization which will give the optimum production. We also want to determine the causes of fluctuations in abundance and the critical period for survival. If these are known it may be possible to stabilize or even increase production.

Much of our menhaden research to date has been concerned with the biological characteristics of the population, determined by systematic sampling of the commercial landings at the major fishing ports throughout the fishing season and studies on the larvae and juveniles during their estuarine residence. Our sampling data permits us to determine the number of menhaden of each age in the catch, their average length and weight, the proportion of males and females, and the relative abundance of each year class. We recently have started a large-scale tagging program on Atlantic menhaden. We insert a small metal tag into the body cavity of the fish and these tags are recovered on magnets in the fish meal plants. This study will provide us with valuable data on the mortality rates of menhaden and information on menhaden migrations. These data, along with data on the fishing effort, form the basis for management of this resource. We have not had the facilities and personnel, however, to undertake the extensive research still required in the Continental Shelf waters, which will require extensive collections of oceanographic data over a wide range of space and time. Synoptic temperature and salinity data from a large area of the coast are needed to understand menhaden migrations better as well as to assess the effect of environmental factors on spawning and egg and larval development. Extensive data are required on ocean currents to learn the method and pathway menhaden larvae use to travel from the spawning grounds into the nursery areas. Also a knowledge of the food chain and the energy processes involved are prerequisite to any attempt at altering the environment for cultivation of the resource or artificial rearing of the larvae. Extensive research vessel time and data from an extensive buoy system, or both, are needed in this work.

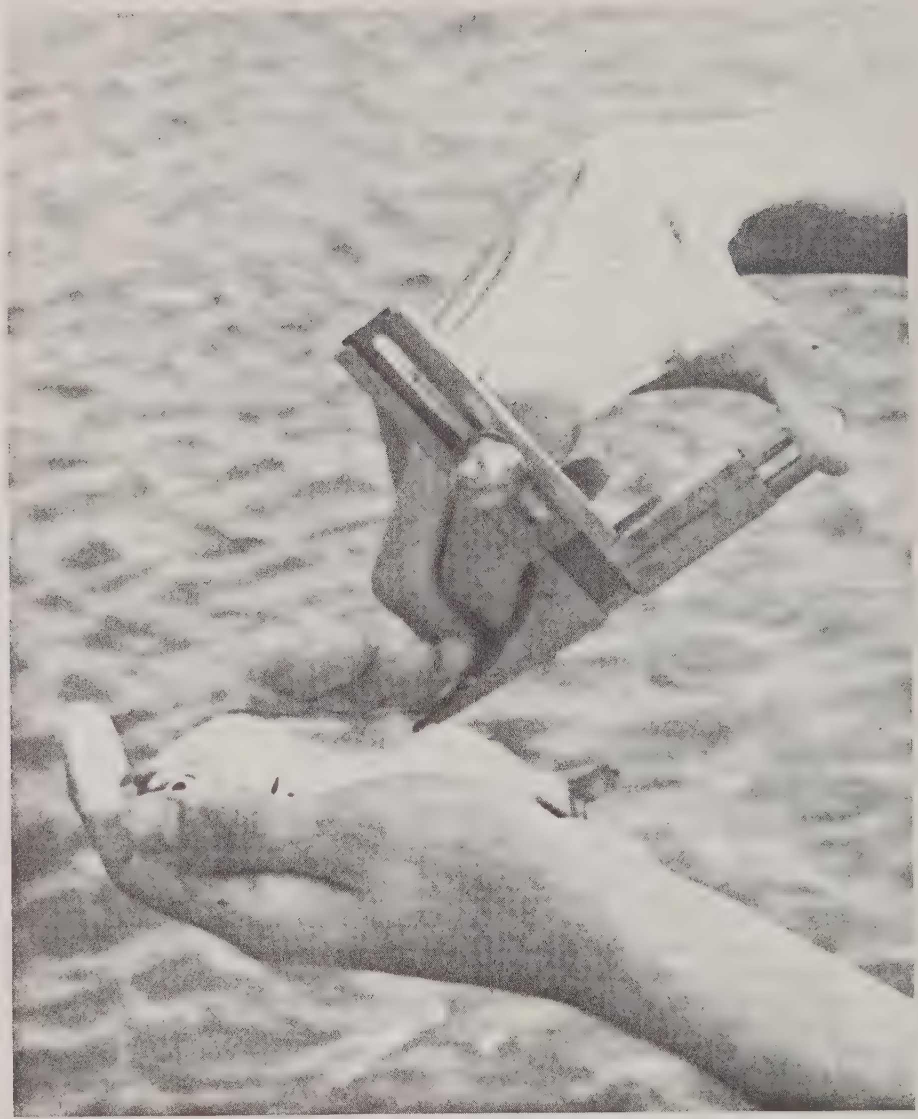

Figure 4.--Tagging an Atlantic menhaden with a metal internal tag.

To summarize this paper briefly, the menhaden is a major resource extending over a wide area of our Continental Shelf waters of the Atlantic and Gulf of Mexico. The resource appears to be fully utilized and the Atlantic stock is currently in a period of sharply reduced abundance. Additional research on these fish will require the collection of synoptic oceanographic and biological data over a wide area of the coastal waters.

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UNDERWATER PHOTOGRAPHY IN THE STUDY OF FISH BEHAVIOR

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Abstract

Slides and motion picture excerpts were used to demonstrate some applications of photography in the study of fish behavior. The problems of avoidance of a purse seine net by fishes, the associations of fish with floating objects, shark behavior, and fish schooling behavior served to illustrate the techniques. Special methods were discussed such as time-lapse photography to record changes in patterns of behavior and infrared photography to observe schools under low illumination.

Introduction

Our Bureau has great interest in fish behavior because knowledge in that field can aid in catching fish faster and in greater quantity. Characteristics of fish behavior determining the size and organization of schools, the avoidance of fishing boats and gear, and the attraction to certain objects are being studied by our laboratory's scientists. Photography is one of the most valuable methods for recording observations in the field and in the laboratory. Since most of our work requires the observation and analysis of the movements of animals it is natural that much of our data collecting is done with underwater motion pictures.

Photography has several advantages for studies of behavior. It provides us with documentary records of behavior in the field which can be analyzed later and in detail ashore. (The observer can record far more information and details on film than he can hope to remember or record verbally or graphically.) Remote, time-lapse photography permits us to extend observations over time limits that would exceed the endurance of a diver. Finally, by combining special film, filters, and lighting we have been able to record fish behavior under conditions where the usual methods would be unsatisfactory..

Observing the fish, however, is not the whole story. Much of our study of fishing-gear avoidance behavior requires the measurement of factors that determine the underwater sighting ranges of nets, other fish, predators, and prey. We have used several types of instruments for visibility studies, but primarily we have depended on photographic techniques. For the remainder of this paper I will touch on several of our projects which illustrate the use of underwater photography in determining underwater visibility and in the study of fish behavior.

Net Visibility

Most of the fish we are working with are caught by a fishing method called purse seining in which a fish school is encircled with a large net and the bottom of the net is closed, or pursed, to prevent the fish from escaping. An understanding of the avoidance of these purse seines by fish requires studies in underwater visibility (Ref. 1) in which we observe the avoidance reaction of the school and calculate the sighting range of the net under varying conditions of water clarity and net color. We have found a 35-mm still camera to be the most convenient and inexpensive instrument for this work. The film exposure is calibrated against a gray-scale target board of known reflectances. From underwater photographs, analyzed with a micro-densitometer, we are able to measure contrast degradation in the water mass and the reflectance of various types of nets and to arrive at some estimate of underwater sighting ranges. All that was required in the field were a small camera, a target board, a measuring string, and a pair of divers.

A second problem of visibility is measurement of the brightness distribution of underwater backgrounds. At the suggestion of the

Visibility Laboratory of the University of California, we obtained a Paxar-Periphoto[1] 180° wide angle lens and mounted it on a 35-mm underwater still camera. This camera allows us to record in one photograph the brightness distribution in an underwater hemisphere for later analysis by densitometry. Again, the field approach is simple, yet the data are sufficiently precise for laboratory work.

Fish Associated with Floating Objects

A remarkable phenomenon and one of considerable importance to fishermen is the attraction that floating objects seem to have for a variety of different fish. Tunas, for example, frequently concentrate near floating logs or school with whales and large sharks. We have been particularly interested in fish-log associations and have devoted several cruises to their study. Two phases of this work required underwater photography. The first was the documentation of the behavior of the animals with still and motion picture cameras. Since we were working near the surface and in daylight no special technical problems were encountered (Ref. 2).

The second phase--measurement of the rate of recruitment of fish to the logs--however, did present problems. Our solution was to equip a number of logs with underwater, time-lapse cameras. These units were built at a cost of $125 each at our laboratory from used 16-mm, magazine-load, motion picture cameras mounted in plastic housings. With the original spring wind and exposure of one frame per minute, these untended units monitored the changes in numbers of fish under a log for 6-1/2 hour periods (Ref. 3).

Shark Behavior

In several of the fishing areas off the west coast of Central America, sharks do considerable damage to the fishing gear. At one time we attempted to find effective methods for repelling or controlling sharks. Again we were faced with documentation of the behavior. The near-surface photography presented no technical problem, but divers had to be protected by a cage or a submersible craft.

Laboratory Studies - Schooling

More than half of our work in our Behavior Program is done ashore. The bulk of our laboratory work has been on the various aspects of schooling behavior. Out of this research has come a unique method of collecting and analyzing schooling data with photography (Ref. 4).

Vision is the key to the formation and maintenance of a school. In the species which have been studied, schooling broke down in the dark. To quantify the dependence of schooling on light, our problem was how to observe the fish in the dark.

The facility for this experiment consisted of a concrete-block room constructed on a foundation separate from the rest of our experimental aquarium to isolate it from outside noise and vibration. The room was light-tight. The floors, walls, ceiling, and all structures in the room were painted with photometric sphere paint to provide a uniform background throughout. The illumination in the room could be closely controlled. Fish behavior was recorded by a 16-mm, time-lapse camera placed in a port in the ceiling of the room above a shallow plexiglass tank.

Kodak high-speed infrared film was used to photograph the fish. Three quartz-iodine lamps equipped with Corning infrared filters illuminated the tank for photography. Despite the high absorption loss in the water in the tank, satisfactory records of the location of individual fish or their schools were obtained without disturbing them. The films were analyzed with a coordinate reader and digitizer which allows very rapid analysis (Ref. 5).

The approach was similar in an outdoor tank 25 feet in diameter to study reaction times in fish schools. Here a continuous time-lapse film record was made by an overhead camera, supported on a tripod high enough to allow full coverage of the pool area. Natural light was used and again the records were analyzed on the coordinate reader. This experiment enabled us to determine the critical angular displacement of one fish in a school which would elicit a response in its partners.

I have confined my discussion to some of the photographic problems we have met in the studies of fish behavior at the Fishery-Oceanography Center, La Jolla. Of course, many other people are working on fish behavior elsewhere. Almost always however, their problems and ours are closely similar and technically simple to solve. Within certain limits of water clarity and illumination, recording by photography has proven to be an excellent method and accordingly is widely used. I believe that the ubiquitous box in the plastic bag will still be around even when new methods in acoustics and electronics have been perfected.

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[1] The use of a trade name does not imply endorsement by the Bureau of Commercial Fisheries.

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VISUAL CONTRAST THRESHOLDS OF THE GOLDFISH (*CARASSIUS AURATUS*)

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INTRODUCTION

The visual sense in fishes has been the subject of numerous investigations. These have included studies of size, shape, form, and color discrimination; examination of fish-eye dioptrics; and electrophysiological, histological, and behavioral investigations of light and motion perception and of visual acuity. Visual acuity may be considered a special case of contrast discrimination—the ability to distinguish a target from its background because the target is lighter or darker than the background.

The ability of a fish to detect an object by contrast discrimination has not been quantitatively measured, but it may be the most important factor in any visual system. Furthermore, contrast transmittance is much poorer in water than in air. Even in the clearest water most targets are visible for only a few tens of meters. Underwater sighting ranges can be calculated readily if certain characteristics of the water mass are known (Duntley, 1963), and if the contrast sensitivity of the observer is known. Once the contrast sensitivity of fishes is determined, many problems are open to solution, among which are spacing of the individuals in a school, object avoidance, predator avoidance, and food detection.

Denton and Nicol (1965) suggested that silver-sided fishes may be difficult for predators to detect because they so nearly match the brightness of their water background. The effectiveness of this camouflage can be determined only when the contrast sensitivity of the predator is known. Baylor and Shaw (1962) suggested that the double-cone mosaics in the teleost retina increase contrast sensitivity. Briggs and Hatchett (1965) pointed out that, because contrast transmission in water is so poor, it would not be surprising to find better contrast discrimination in fishes than in terrestrial vertebrates, but did not suggest a mechanism whereby the sharper discrimination could be brought about.

In the light-adapted human eye, contrast thresholds are lowest at the fovea and increase toward the periphery of the retina in rather good agreement with the number of cones in the corresponding retinal regions (e.g. Blackwell and Moldauer, 1958; Taylor, 1961). Since the cone density in the teleost retina, even in pseudo-foveate species, is at most about 10 per cent of the human fovea (Tamura, 1957; O'Connell, 1963), it seems unlikely that fish eyes have lower contrast thresholds than the light-adapted human fovea.

Contrast, as used above, can be defined as the ratio of the difference between the radiance of an object and its background to the radiance of the background. The more usual way of defining contrast is to use brightness or luminance instead of radiance. These terms, however, are based on the sensitivity of the human eye and are difficult to interpret when the detector, the fish retina, may have a different spectral sensitivity. The use of radiance surmounts this difficulty, since the units are in actual units of energy for a specified band of wave lengths within the visible spectrum for the organism.

Contrast can assume any value from —1 (when the target radiates no flux and the background does) through zero (when the target and background have equal radiance) to some large positive number (when the radiance of the target is large with respect to the background). Threshold values of the light-adapted human eye for stimuli of moderate area typically are fractional and are distributed symmetrically on either side of zero. Under usual conditions, the threshold is independent of whether the target is lighter or darker than its background; only the absolute value of contrast is important (BLACKWELL, 1946). This generalization greatly simplifies the problem of target generation and measurement. That is, the test object may be a spot projected on a background of some uniform radiance. In the procedure outlined below all the contrast values are positive. This arrangement has the additional advantage of permitting the use of contrast values greater than unity. Such values do occur in nature and are especially important at low adaptation levels, and for objects that subtend small angles in the visual field.

Contrast threshold values for the human eye vary with target size, position of the target image on the retina, and the radiance level to which the eye is adapted, as well as with duration and color of the stimulus. (The latter two are not considered in the present study.) It is highly probable that similar relations will be found to hold for fishes. For this reason a contrast discrimination experiment on a fish, to yield useful data, should involve targets of several different areas, should cover a wide range of adaptive states from full-dark to full-light, and should examine several regions of the retina. This last point is especially important for experiments with most fishes, since their visual field is extremely large and nearly spherical, and since visual stimuli can operate anywhere in this field.

Two other considerations, stimulus duration and the subject's spectral sensitivity, arise when experimental techniques used on humans are transferred to fishes. The human eye covers a search field in a series of steps, each of which ends in a brief pause before the point of fixation is again shifted in space. For a stimulus to be "realistic" its duration should be the same as the dwell time of the eye. Since reportedly the typical fish eye remains fixed in space, and ocular movement compensates only for body-swimming movement (WALLS, 1942), a suitable stimulus duration for the fish must be chosen arbitrarily. It should not be so short as to be unrealistic and yet should not be so long that natural moving targets, such as other fish, will appreciably change position, or that prey will have time to sight the fish and escape. An arbitrary duration of 0·5 sec seems to fulfill the above condition as a first approximation.

The spectral sensitivity of the human eye, for both light- and dark-adapted (photopic and scotopic) vision, has been standardized and a science of measurement based on this sensitivity—namely photometry—has been developed to a high degree. Fish photometry is, at best, poorly defined. Spectral-sensitivity curves for fishes are based chiefly on pigment-absorption spectra, such as those reported by BAYLISS, LYTHGOE and TANSLEY (1936), MUNZ (1958), and WALD (1941), and apply primarily at low-adapted (scotopic) levels. The behavioral studies (for example, by GRUNDFEST, 1932) and electrophysiological studies (GRANIT, 1941) demonstrate a shift in the peak spectral sensitivity between light- and dark-adapted eyes in several species of fish (a frequent response in a duplex retina). These sensitivity curves show marked interspecific differences. The only warranted generalization is that the curves for fresh-water and inshore fishes generally are more red-sensitive than those for pelagic and deep-sea fishes. Since the curves for all fishes examined differ from those for the human eye, photometric expressions of stimulus and background levels appear to be of doubtful meaning. Water is an excellent monochromator, however, so that underwater light in most natural waters below a few meters of depth is confined to the blue-green portions of the spectrum. These wave lengths can be approximated in the laboratory by the use of proper narrow-pass filters such as a Wratten 611, with peak at 534 mμ, to simulate underwater light in fresh-water and near-shore water, and a Wratten 45, with peak at 480 mμ, to simulate oceanic water. By use of such filters, radiance measurements can be made with reasonable accuracy and the interspecific differences and the differences due to the duplex nature of the retina are reduced to some common physical measure.

Under certain circumstances, color discrimination may affect contrast discrimination (McCLEARY and BERNSTEIN, 1959, and others have demonstrated color vision in fishes). For the human eye, however, and probably for that of fishes, the visibility of objects depends primarily on luminance contrast at all levels of illumination, and entirely on luminance contrast at low levels of illumination, at which color vision is inoperative (MACADAM, 1946). Chromatic contrast is undoubtedly of even less importance in the aquatic environment, due to the rapid loss of all but a narrow band of wave lengths below a certain depth; it can be eliminated completely by the use of narrow-pass filters.

At least one visual function in fishes, namely critical flicker fusion, is known to be temperature dependent (CROZIER, WOLF and ZERRAHN-WOLF, 1938; TAMURA and HANYU, 1959; HANYU and ALI, 1963). Similar temperature effects should be considered in contrast threshold experiments and should be controlled carefully (a need that does not arise in experiments on human vision).

As the eye of the fish grows, the density of cones declines more slowly than is required to compensate for the calculated expansion of the image area in the larger eye (TAMURA, 1957; LYALL, 1957; O'CONNELL, 1963) leading to increased acuity or sensitivity, or both, in larger fish of any species. Such an increase in acuity with growth has been reported in the cichlid *Aequidens portalegrensis* (BAERENDS, BENNEMA and VOGELZANG, 1960). The size of the fish, then, should be considered when any visual data are collected.

Some of the most interesting problems open to analysis when contrast threshold data are available pertain to the open ocean, where sighting ranges are relatively great and vision probably plays an important role. It is therefore desirable that experiments on contrast thresholds be run on open-water fishes. This initial study, however, has been so complex that additional complications caused by choosing a subject that is difficult to obtain and maintain have been avoided. Pelagic fishes in general are not easy to work with; some of the more interesting ones require special life-support systems, and even then they show a disturbing inclination to die at the most inopportune time. Near-shore species are easier to collect and keep but also require salt water, which is highly corrosive to electronic equipment. These difficulties have been avoided by choosing the goldfish, *Carassius auratus*, one of the many hardy and readily available fresh-water fishes that have been widely used in previous behavioral and physiological investigations, and a species that has been the subject of several studies pertinent to the present investigation.

METHODS

Apparatus

In the apparatus (Fig. 1) used throughout the studies the fish is held in a vacuum-formed plastic holder

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[1] The use of a trade name does not imply endorsement by the Bureau of Commercial Fisheries.

in a plastic tank. The holder was so designed that the anterior part of the fish, including the eyes, is free, but the fish is immobilized. The holder and fish can be rotated, raised and lowered, so that nearly every part of the visual field can be directed toward one end of the tank.

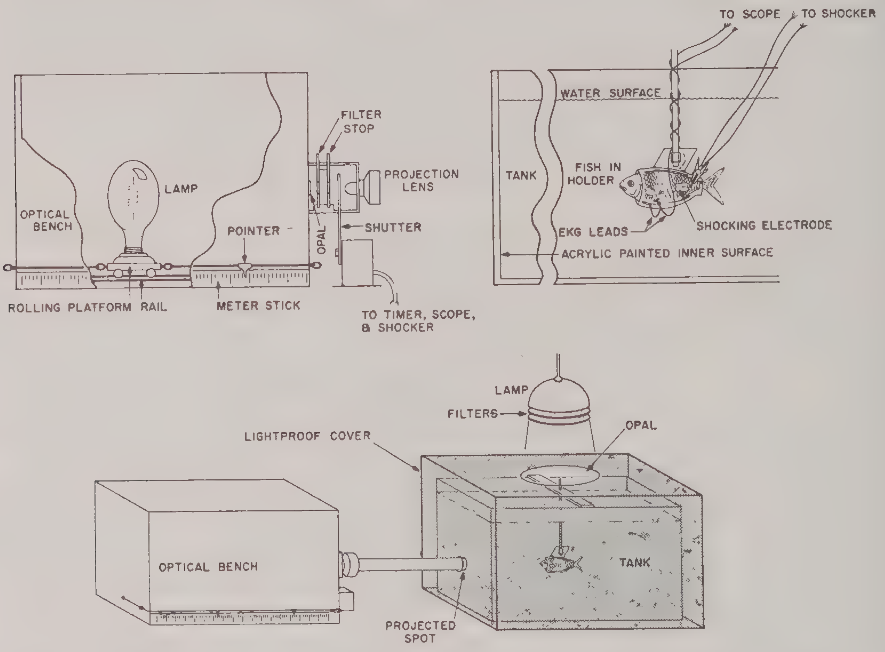

FIG. 1. Apparatus used in the determination of contrast thresholds of the goldfish.

The inner surface of the tank in which the fish is held is coated with a white acrylic paint. A thin layer of this paint acts as an effective diffuser, yet allows the conditioned stimulus, a spot of light, to be projected upon it from outside the tank, with little edge degradation.

The tank is covered by a sheet of opal plastic and is lighted from above by a single tungsten-filament lamp. This lamp is equipped with a water-bath filter; a narrow-pass filter, Wratten 61 (peak λ 533·8 mμ); and neutral density filters as required. This combination of tank, diffusers, light, and filters provides rather uniform radiance distribution, varying less than 20 per cent on the walls and bottom of the tank. The measured radiance of the end of the tank on which the target is projected (see below) is the background radiance used for calculating target contrast and also the adapting radiance for the subject.

A circular target can be projected on one end of the tank by opening the electronically controlled shutter on the optical bench. The spectral content of this stimulus is set by a Wratten 61 filter. The diameter of the target is varied by a series of optical stops. Stepwise adjustment of the target radiance is regulated by neutral-density filters. The optical bench provides fine adjustment of the target radiance over a 1·4-log range.

An electronic timing device was constructed to control both the shutter and an electric shocker, the unconditioned stimulus. The time sequence used was 0·5 sec open for the shutter and 0·2 sec on for the shock. The shock was timed to occur 0·4 sec after the shutter opened. During training, the time between stimulus presentations was controlled by a motor-driven potentiometer and varied from 40 to 60 sec, with a mean of 50 sec. During data runs the inter-trial interval was fixed at 45 sec.

Radiometry

The radiance of the tank interior and the projected spot were measured with a Gamma Scientific Model 200 M log-linear photometer equipped with a fiber-optic probe which allows measurements to be made underwater. The photometer was calibrated with a Gamma Scientific Model 200 luminance standard and Wratten 61 filter. The standard was calibrated with an Eppley thermopile. The cumulative calibration error for absolute measurements was estimated to be ±20 per cent.

Contrast as previously defined is $C_0=\frac{N_t-N_0}{N_0}$, where N_t is the radiance of the target and N_0 is the radiance of the background. Target radiance was measured independently of background radiance ($N_0=0$).

Computed values for C_o were reproducible to within ± 5 per cent.

The fish holder was positioned 40 cm from the target-end of the tank. The water in the tank had a spectral volume attenuation coefficient $\alpha_{533} \sim 0{\cdot}40$, measured with a Marine Advisers alphameter having a 1-m path length. Contrast transmittance in a scattering and absorbing medium is given by $\frac{C_r}{C_o} = e^{-\alpha r}$ (DUNTLEY, 1963) where C_o is inherent contrast measured at the target, C_r is apparent contrast measured at distance r (the distance from the observer to the target), e is the base for natural logarithms, and α is the spectral volume attenuation coefficient. Computed C_o was corrected for the 40-cm path by the factor 0·85 to obtain C_r.

Psychophysical methods

There are three classical methods of determining psychophysical thresholds: the direct method or method of adjustment, the method of limits, and the method of constant stimuli or indirect method. There is no reason to expect the threshold obtained by these three different methods to be the same. The direct method is usually based on the dispersion of the observed values as measured by the standard deviation. The method of limits takes the arithmetic or the geometric mean between the upper and lower stimulus intensity. The indirect method is based on the medium of an ogive calculated from the experimental data. HOLWAY (1937), however, related the direct method and the indirect method through Crozier's Law $\frac{\sigma}{T_{0.50}} =$ a constant. The method of limits is more subject to the observer's criteria of "just perceptible' and "just imperceptible" and usually results in a higher threshold than is obtained with the other two methods.

These then were the three choices for determining contrast thresholds of the goldfish. The method used was determined from the requirements of the experiments and the physical ability of the subject. The method of limits was not considered since thresholds obtained in this manner are difficult to relate to the thresholds obtained with the other two methods. Of the remaining two, the method of constant stimuli was selected for the present study because it is generally considered to be the most desirable (BLACKWELL, 1952), since the threshold is computed rather than specified by the subject.

Because careful control of target diameter, location, and contrast were required, the movements of the goldfish necessarily had to be restricted. Immobilization precluded use of the usual motor responses ordinarily preferred by animal psychologists; instead, the cardiac response suggested by OTIS, CERF and THOMAS (1957) was chosen. A second reason for choosing the cardiac response was that the method of constant stimuli requires many observations for each set of data points. An additional advantage of cardiac response over motor response is that conditioning is more rapid; consequently many trials can be made in a short time.

There are two ways to conduct an experiment in which the method of constant stimuli is used. One is to require the subject to make a phenomenal report of the stimulus: respond "yes" if the stimulus is perceived and "no" if it is not. The second is to require a forced-choice: the subject giving some verifiable attribute of the stimulus other than whether or not it is perceived. BLACKWELL (1952), in his discussion of psychophysical methods, concluded that data obtained by forced-choice are generally superior to data obtained with the yes–no response. The difficulties in devising a forced-choice experiment for goldfish in which the cardiac response is used seemed to outweigh the benefits expected from the increase in the precision of the data. Instead the stimuli were presented at unexpected intervals and a yes–no cardiac response was recorded.

Conditioning and response

The method used to determine stimulus perception was an adaptation of the classical conditioning described by OTIS, *et al.* (1957). The goldfish was placed in the holder, wired, and positioned in the tank so that the desired part of the visual field was directed toward the end of the tank where the target would appear, a distance of 40 cm. The electrocardiogram electrodes were two insulated #22 copper wires with bare tips, one of which was placed on each side of the body beneath the pectoral fins. To avoid damage to the subject, the electrodes were in contact with the sides of the fish, rather than implanted.

Heartbeat was monitored on one channel of a Tektronix 564 storage oscilloscope with a type 3A3 dualtrace differential amplifier and a type 2B67 time base. The other channel was used for the conditioned stimulus marker. The EKG so obtained could be stored and photographed. The output of the oscilloscope preamplifier was also fed to a Sanborn 299 d.c. amplifier-recorder.

After the fish was properly positioned it was allowed to acclimate for a short period until the heartbeat was normal. Conditioning was effected by using the target with an angular subtense of 194′ of arc at a contrast level sufficiently high to produce an orientation response. The target was presented for 0·5 sec. After 0·4 sec a mild shock, 0·2 sec in duration, was given the fish. The shocking voltage, typically 3·0 V d.c., was adjusted to produce a strong cardiac inhibition. The interpresentation interval was randomized ±10 sec about a mean value of 50 sec. Conditioning usually required 15–20 training presentations.

After the fish was conditioned, the target contrast was decreased to a low level and raised in 0·3-log increments until a response was noted. The fish was then tested at a contrast level 0·1 log lower for 5 trials and the number of responses noted. If the number of responses was 2 or 3, making this contrast near the 50-per cent response level, a higher and a lower 0·1-log increment of contrast were taken to give three contrasts, 0·1 log apart, that included the level of approximately 50-per cent response.

The fish was then reinforced 3 times and tested with 5 trials at each of the 3 levels of contrast, reinforced 3 times, and retested until 25 trials were run at each of the 3 levels.

During testing, due to the nature of the recording apparatus, it was desirable to change the inter-trial interval to a fixed period of 45 sec. Since the responses were always below the 90-per cent level it can be argued that this procedure did not result in the subject's anticipating the time of stimulus onset.

The conditioning described above resulted in a generalization of the stimulus by the subject. Fish conditioned to the 194′ target responded to targets of smaller dia. and targets located elsewhere in the visual field. In addition, fish conditioned binocularly responded to targets in the monocular field; however, in the experiments involving the monocular field the fish was conditioned with one eye covered.

The 3 contrasts in an experiment were presented in a random order, and 5 trials were run at each contrast. After 2 sets of 5 trials, each fish was reinforced 3 times at a higher contrast. The last 3 sets of 5 trials each were run consecutively without reinforcement. The 3 contrasts were presented in a fixed order, low to high. When this schedule of trials and reinforcements was used, extinction never was apparent.

McCleary and Bernstein (1959) used the cardiac response to demonstrate color vision in the goldfish. In their experiments the stimulus duration was 10 sec. Response was measured by comparing statistically the number of heartbeats counted during this 10-sec period with the number counted during a 10-sec period throughout which a neutral stimulus was presented. For the stimuli of short duration used in the present study, the cardiac response was markedly different. The heart rate was constant except immediately after stimulus presentation, when only one or occasionally a few beats were skipped or were of decreased amplitude. Statistical comparison of the number of beats following stimulus presentation and the number of beats during some other period were not significant; however, the single-beat inhibition was so pronounced (Fig. 2) that it alone was a reliable indication of response.

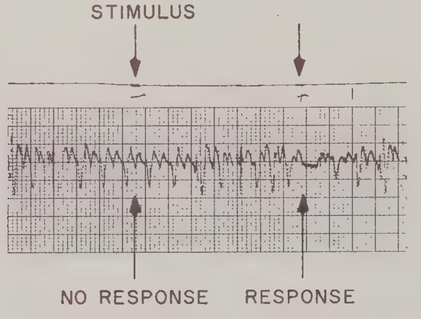

Fig. 2. EKG recording from a goldfish showing the cardiac response to a circular spot of light having a duration of 0·5 sec, a contrast of 0·26, and an angular subtense of 194′ of arc. Background radiance was 0·07 $\mu W\overline{cm}/^2/\omega$.

Regardless of the contrast level used, there was no tendency for an increased latency or a decreased amplitude. Similarly, latency and amplitude changes were not noted during the experiments in which temperature and consequently heart rate were higher or lower. The cardiac response reflected the all-or-none character of the visual phenomenon over the entire range of contrasts. The response seemed to be an excellent and easily observed indicator for yes–no phenomenal reporting.

Unfortunately, the initial success of the technique did not continue throughout the course of the experiments. The number of conditioning failures was near a constant 20 per cent for all the experiments at the 3 highest adaptive levels. Some of the subjects (and the experimenter) had bad days but the same subject often performed well at a later date. When the adaptive level was lowered to 0·07 $\mu W/\overline{cm}^2/\omega$, the rate of failure increased slightly: several reliable subjects no longer performed well; the heartbeat of one fish, a veteran of some 20 sessions, became erratic; and other fish would not condition at all. Despite these difficulties it was possible, by using new subjects, to complete this series of experiments. At the next lower level, 0·007 $\mu W/^2\overline{cm}/\omega$, the rate of failure was 100-per cent. The experiments were terminated at this point.

Processing of psychophysical data

Biological assay is a term meaning the measurement of the potency of any stimulus by means of the reactions which it produces in living material. Often the response is quantal; that is, an all-or-nothing response—as in the goldfish experiments, in which a cardiac response is or is not elicited by a given stimulus. Probit analysis provides a method of statistically treating quantal biological assay data.

The history of the probit method was thoroughly discussed by FINNEY (1952). Although probit analysis has been widely used, the calculations are tedious and many workers have resorted to a graphical method. Recently RICHARDSON (1967) and others have developed computer programs for probit analysis that greatly speed the calculations.

BLACKWELL (1953), in a study of the form of visual threshold data, showed that in a series of experiments all the data for four subjects could be fitted by one or another Poisson sum. In the same series he found that the data for three of the subjects were fitted by normal ogives and the data for the fourth were fitted by log-normal ogives. The circumstance that predictions concerning the magnitude of the threshold were not verified by using Poisson sums, however, led Blackwell to conclude that threshold data could probably be analyzed adequately by either normal or log-normal ogives.

BLACKWELL (1953) used a special version of the χ^2 test to determine the number of observations required to separate statistically data log-normal in form from data normal in form. This is the number of observations that must be made to obtain an unacceptable fit to a normal ogive by data actually log-normal in form (or the reverse). If 10 stimulus levels were used in an experiment, 209 presentations at each level, or 2090 observations, would be required.

For goldfish, the contrast threshold was taken to be the contrast at which positive responses were elicited 50 per cent of the time. Typically, each experiment provided data from 25 trials at 3 contrasts. Both a normal and a log-normal probability integral were fitted to these data by the probit analysis computer program of RICHARDSON (1967). The fit was slightly better if the log-normal transformation was used; however, the 25 observations at each of 3 levels used in the goldfish experiments fall far short of the required number (see above). Therefore the lower χ^2 values for the log transformation found in most of the experiments cannot be considered of statistical significance. Either curve will give a good estimate of the threshold (less than 2 per cent difference in most of the goldfish data).

Biological material

The fish used throughout were "wild-type" goldfish, *Carassius auratus*, obtained from a local dealer. They were fed a commercial dry fishfood which they supplemented with the vegetation in their tanks. Day length was artificially controlled, 12 hr light, 12 hr dark. During the experiments at low radiance levels the light-dark in the holding tanks was reversed. Water temperature was held at 20° C (except during one experiment on temperature effects).

All measurements of fish were standard length (tip of snout to base of tail, measured to the nearest mm). The fish were 49–110 mm long. Lens dia. was measured on material preserved in 70 per cent alcohol.

During the study it was customary to use the same group of fish (usually 5) for each particular experiment. When other fish had to be substituted they were selected to approximate the performance of the original subjects as nearly as possible.

Histology

For histological preparations of the retinae, specimens were decapitated, the corneas pierced, and the whole heads fixed in Bouin for 24 hr. The left eye was then removed and enucleated, a snip of the ora was removed for orientation, and the eye was returned to Bouin. After the eye remained in fixative for at least an additional 24 hr, it was cleaned in 70 per cent ethyl alcohol for several days, dehydrated, and cleared in cedarwood oil. The eye was then embedded in paraffin and divided into sections—usually 12, although some additional sections near the ora were taken on one fish. These sections were reembedded and sectioned as near to the center of the convex surface as possible. Tangential serial sections 6–8 μ thick were made and stained with Mallory triple stain. Photo micrographs of the sections were made and the number of single and double cones counted on the photographs. The numbers of cones per $0{\cdot}00125$ mm^2 were counted from 4 locations on each photograph and the total of the 4 counts doubled to get the number of cones per $0{\cdot}01$ mm^2. Whenever possible the average of two or more sections from the serial were used to estimate these numbers.

THE GOLDFISH EYE

Anatomy

The eye-cups of goldfish appear hemispherical, with equal horizontal and vertical axes. The 6 oculomotor muscles are developed, the *inferior rectus* weakly. Both obliques tend steeply inward in the socket, suggesting limited movement of the eye in the equatorial plane. The lens rests against the immovable iris and is suspended dorsally and slightly temporally by the well-developed ligament. The weakly developed *retractor lentis* is attached to the lens ventrally and slightly nasally and runs radially to the retina at the ora. The *retractor lentis* lacks the lateral component necessary to move the lens along the temporal-nasal line. This attachment, however, seemingly could roll the lens inward toward the fundus, but such movement is doubtful, since the muscle is developed so poorly. Furthermore, KIMURA and TAMURA (1966) found that the muscle failed to contract when stimulated electrically. Their results indicate that the goldfish apparently lacks a functional accommodative apparatus; and, indeed, it is difficult to see why one is necessary in a hemispherical eye. According to PUMPHREY (1961), the usual shape of the fish eye-cup is semi-ellipsoidal with the long axis running temporal-nasal. Accommodation of such an eye is effected by a movement of the lens along this axis. The center of the lens of a hemispherical eye-cup is everywhere equidistant from the retina and the image is in equal focus regardless of its angular position in the visual field. This would hold true for objects farther than about 2 m from the fish if the distance from the lens to the retina and the focal length obey Matthiessen's ratio (focal length = 2·55 lens radius·. Objects closer than 2 m would be slightly out of focus.

Presumably the 40-cm target-to-subject distance used throughout the experiments was viewed by the goldfish with the refractive state of the eye constant regardless of the position of the target in the visual field. For a lens having a focal length of 3·3 mm (2·55 × 1·3 mm lens radius) an image on the retina at the *limitans*, of an object at infinity, will be shifted 62 μ toward the sclera when the object is moved to a distance of 40 cm. Since the receptive layer in the goldfish retina is about 40 μ thick, the image of an object at 40 cm will fall outside the layer of visual cells. For large targets this refractive error should have a negligible effect on contrast perception.

The goldfish eye lacks a choroid gland and a falciform process. Instead, hyaloid vessels radiate over the retina from the optic papilla. In the sectioned eye of a 72-mm goldfish having a 7-mm dia. optic cup, the dia. of the papilla was about 0·024 mm. The visual cell layers that surrounded it were compressed over an area about 0·083 mm in dia. In an ophthalmoscopic examination of enucleated, preserved eyes the papilla appears surrounded by radiating lines of nerve fibers overlying the retina. The hyaloid vessels are few but prominent. No tapetum is observable.

The binocular field was measured on two goldfish immobilized in plastic holders. With the eye free to move, the field of overlap was about 45° in the horizontal plane and about 54° for a path of sight directed 15° upward or downward. If the fish were anesthetized with MS 222, so that the eyes were immobile, the binocular field was about 10° narrower.

In anesthetized fish the eyes could be moved in the socket some 60° forward and 20° to the rear and +10° to −50° vertically. Eye movements of this magnitude were not observed in free-swimming fish. These fish moved their eyes somewhat when swimming or when prodded with a pencil. The eye of a fish contained in a holder could be made to follow the spot from an ophthalmoscope. Movements of about 20° forward were observed. Rearward movement was very slight—less than 5°. The eye was not observed to move above the horizontal but did follow the beam downward about 20°. A downward jerk of at least 40° was observed occasionally, apparently associated with a respiratory cleaning movement.

Histology

ENGSTROM (1960) found two types of single cones and unequal double cones in the goldfish retina. In one of his two goldfish he described a distinct pattern similar to the square pattern reported for trout (LYALL, 1957). The pattern in the goldfish is most readily distinguished in the equator of the eye. In my material a pattern is not discernible; the lack of it made cone counts difficult.

In the three whole eyes examined for the present study, double cones are more numerous than both types of single cones combined. Double and single cones are both more numerous in the dorsal and temporal regions than in the nasal and ventral regions (Fig. 3). Rods are presumed to be present, since the absorption spectrum for the dark-adapted goldfish eye has been shown to differ from the photopic spectrum (BURKHARDT, 1966). The photopic curve has a maximum at 560 mμ, whereas the scotopic curve has two maxima, one at 560 mμ and a slightly higher one at 500 mμ. Rods are not discernible in any of my material and must be small. Numerous rod nuclei can be seen in cross-sections of dark-adapted eyes, but counts have not been attempted.

LYALL (1957), MÜLLER (1952), and O'CONNELL (1963) all reported that cone density for several species decreased with retinal growth but at a lesser rate than would be expected if the total number of elements remains constant. Lyall and Müller found new elements being added by mitosis at the retinal margins. If the number of cones in the retina remains constant during the growth of the eye, the number of cones per unit area should decrease proportionally to the increase in area of the retina. The number of cones per unit area then should be proportional to the square of the lens diameter (assuming that Matthiessen's ratio holds) and the regression of log number of cones per unit area on log lens diameter should have a negative slope of −2. If new cones are added in the retina during the growth of the eye, the number of cones per unit area should decrease at a lesser rate, and the slope of the regression log number of cones per unit area on log lens diameter should be between 0 and −2.

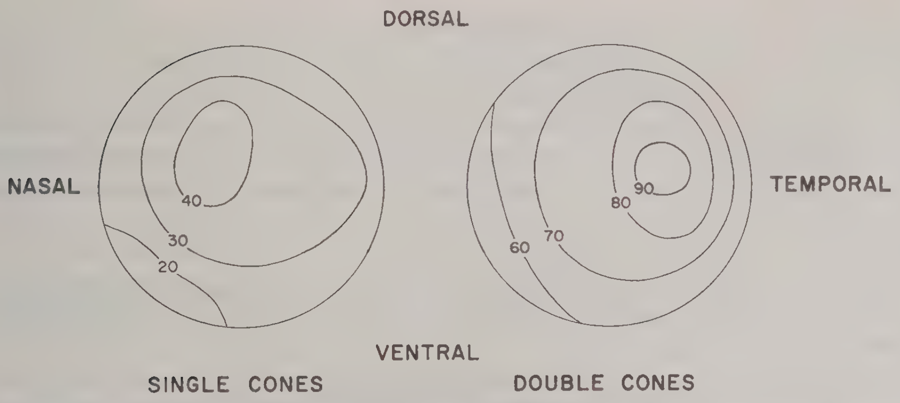

FIG. 3. The probable cone topography of the goldfish retina in number of cones per 0·01 mm^2 of retina. No correction was made for shrinkage.

Single and double cones per 0·01 mm^2 in sections from the ventral-temporal region of the retina were counted for 8 goldfish with lens dia. of 2·40–3·00 mm. The slopes of the two regression lines are −1·53 for single cones and −1·36 for double cones. The variability is so great, however, that neither line differed significantly from either 0 or −2.

RESULTS

Relation of contrast threshold to fish size

The histological examination of the goldfish retina indicates that as the eye increases in size, cone density decreases at a lesser rate than that predicted on the basis of area alone. Similar observations on other species led O'CONNELL (1963) to suggest that some aspects of the visual performance in a fish may vary in relation to the size of the eye. To study the relation of contrast threshold and fish size, binocular contrast thresholds $^{(P=0.50)}$ were determined for 14 fish (49–92 mm standard length), at 20° C. The target subtended 194′ of arc, and was positioned in the binocular field directly in front of the fish at 0° elevation and 0° bearing. Adaptive radiance was 10^2 μW/$\overline{\text{cm}}^2/\omega$.

Fish length and contrast threshold were negatively correlated at a significant level ($r=-0{\cdot}709^{**}$).[2] The comparison of lens dia. with length shows sufficient variation to suggest that lens dia. is a better index of visual performance; the correlation is improved considerably ($r=-0{\cdot}819^{**}$)[2] for the new regression (Fig. 4):

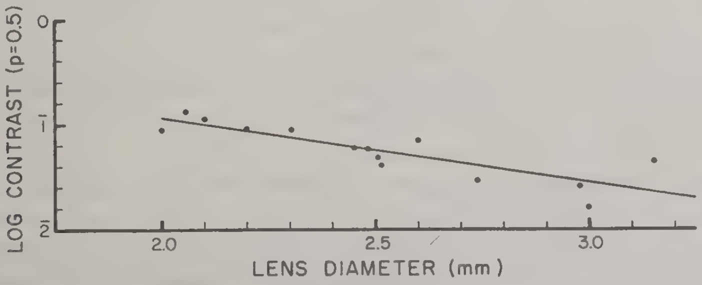

FIG. 4. The relation of contrast threshold to lens diameter for 14 goldfish. The line is the regression equation $y=-0{\cdot}60x+(0{\cdot}230)$.

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[2] Significant at the 0·01 level.

$$y = -0{\cdot}60x + (0{\cdot}230)$$

where $y = \text{log threshold}^{(P=0.50)}$

and $x = \text{lens dia. mm.}$

These data suggest that the performance of at least one visual task, namely contrast perception, improves with growth, confirming the observations of BAERENDS, *et al.* (1960) who reported an increase in acuity with growth in the cichlid *Aequidens portalegrensis.*

Relation of contrast threshold to temperature

Because the relation between threshold and eye size was significant, goldfish of approximately the same standard length (70–90 mm) were used in this and the following experiments.

Binocular contrast thresholds $^{(P=0.50)}$, were obtained for 5 fish at 15, 20, 25, 30, 35° C. Target dia. was 194′ of arc. Adaptive radiance was $10^2\ \mu\text{W}/\overline{\text{cm}}^2/\omega$. The fish were allowed to acclimate for at least 48 hr at each temperature except 35° C. Thresholds at 35° were taken by using fish acclimated 48 hr at 30° C, raised to 35° C during 1 hr, and acclimated at 35° C for 1 hr. Threshold was lowest at 20° C and increased at higher and lower temperatures (Fig. 5).

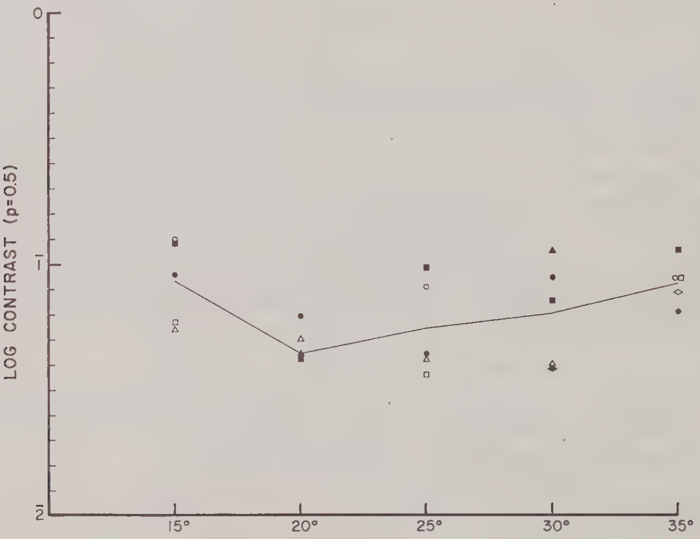


FIG. 5. The relation of contrast threshold to temperature. Each symbol performance for an individual fish.

Two aspects of vision have been shown to be temperature-dependent in poikilotherms. CROZIER, *et al.* (1938) found that critical intensity for the turtle *Pseudemys* was decreased if temperature was increased from 21·5° C to 29·5° C and flash frequency was held constant. HANYU and ALI (1963) described a linear increase in the maximum flicker fusion frequency of the goldfish over a temperature range of 5–25° C.

AREY (1916) found more uniform pigment distribution in the light-adapted goldfish retina at 25 than at 5° C. In the retina of dark-adapted goldfish, pigment contraction was less at the lower temperature. Arey also found an increase in the elongation of the chief cone myoid of the double cones at the higher temperature. The accessory cone myoid did not change with temperature.

The threshold temperature data for the goldfish suggest that the mechanisms linking the two operate more efficiently at 20° C than at the higher or lower temperature. The relation between flicker frequency and temperature reported by HANYU and ALI (1963), however, showed no inclination to change in slope even at 25° C. Although no clear relation exists between flicker-frequency and contrast perception, their observations suggested that the mechanism responsible for the threshold minimum at 20° C might be at least a step removed from processes in the retina.

At least two temperature related phenomena in the goldfish have been shown to be maximal near 20° C. FRY (1957) found that the scope for activity, the difference between the active and standard metabolism of the goldfish, was maximal at about 27° C. In a later study BEAMISH and MOOKHERJII (1964) reported a maximum at 20° C in the average routine oxygen consumption of the goldfish; they attributed this maximum to an increase in spontaneous activity at 20° C.

Relation of contrast threshold to retinal position

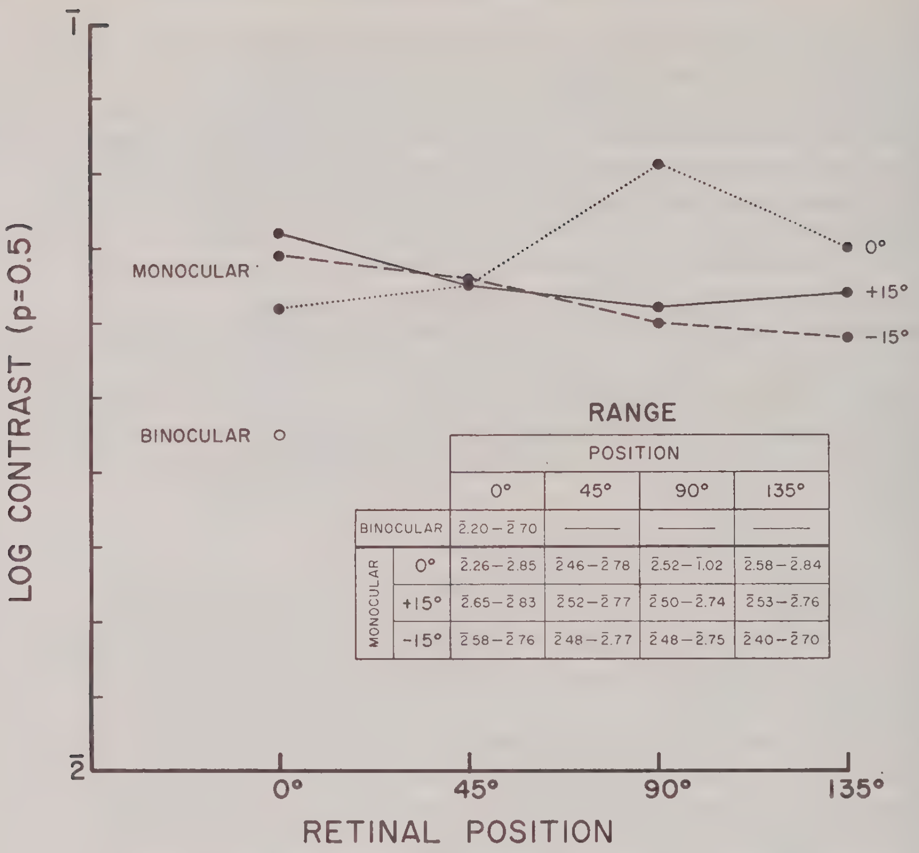
The nonuniform cone density of the goldfish eye suggested that differences in contrast threshold depend on the position of the image on the retina. Threshold differences (Fig. 6) appear to be related to cone density. The fish were immobilized in the usual manner and the contrast thresholds were obtained for the binocular field, with target at 0° elevation and bearing. Monocular contrast thresholds were also taken with the target at 12 different positions in the visual field: 4 in the horizontal plane, 4 with the fish in the plane 15° below the target and 4 with the fish in the plane 15° above the target. Bearings of 45° increments measured from the nose also were used. Target dia. was 194′, temperature was 20° C, N_o was 10^2 $\mu W/\overline{mc}^2/\omega$. Monocular thresholds were taken with a blinder over the right eye of the fish; the left eye was uncovered and both eyes were free to move in their sockets.

The goldfish data show that the difference between the binocular and monocular threshold is about 0·17 log units (binocular threshold = 0·67 monocular threshold). LE GRAND (1957) discussed the difference between monocular and binocular threshold in terms of a simple summation of probabilities. If the assumption is made that at any instant there is no correlation between the sensitivities of the two eyes, the calculated ratio of binocular to monocular thresholds for the goldfish is 0·68 monocular threshold, a difference of 0·17 log units—in good agreement with the data.

Monocular threshold in the horizontal plane increased at the center of the eye. Since the area of the retina covered by the target image included the optic papilla, an increase in threshold (decrease in sensitivity) might be expected. A target with a dia. of 194′ of arc would project as a spot approximately 0·15 mm in dia., on the retina of an eye 7 mm in dia. The diameter of the papilla in an eye this size was 0·024 mm (0·083 mm across the region of retinal deformation). Thus, the target covers an area of the retina considerably greater than that of the papilla.

The average monocular threshold for an upward or downward path of sight decreased slightly toward the center of the retina. This decrease might be related to the increase in cone density toward the center of the eye (Fig. 3); however, additional complications were found to be involved which makes these two data sets suspect.

A similar relation—a lower threshold in regions of high cone density—has been described for the human eye (TAYLOR, 1961). JACOBSON and GAZE (1964) and SCHWASSMANN and



RANGE

		POSITION			
		0°	45°	90°	135°
BINOCULAR		$\bar{2}.20-\bar{2}.70$	———	———	———
MONOCULAR	0°	$\bar{2}.26-\bar{2}.85$	$\bar{2}.46-\bar{2}.78$	$\bar{2}.52-\bar{1}.02$	$\bar{2}.58-\bar{2}.84$
	+15°	$\bar{2}.65-\bar{2}.83$	$\bar{2}.52-\bar{2}.77$	$\bar{2}.50-\bar{2}.74$	$\bar{2}.53-\bar{2}.76$
	−15°	$\bar{2}.58-\bar{2}.76$	$\bar{2}.48-\bar{2}.77$	$\bar{2}.48-\bar{2}.75$	$\bar{2}.40-\bar{2}.70$

FIG. 6. Variation of contrast threshold for different positions of the target in the visual field. Each point is the mean for five fish. Target position in degrees is measured in the horizontal plane from directly in front of the fish (0°) rearward in the visual field to 135°. The points are for monocular thresholds—the dotted line for paths of sight in the horizontal plane, the solid line for paths of sight directed upward 15°, and the dashed line for paths of sight directed downward 15°. The open circle is the mean binocular threshold, target in the horizontal plane at 0° bearing. The log of the ranges for each point is given in the table.

KRUGER (1965), however, did not find areal differences in flash perception on the goldfish retina in the optic tectum, and concluded that there was no indication of a specialized area in the visual field in this species.

Relation of contrast threshold to target size and adaptive radiance

Binocular contrast thresholds were obtained for groups of fish at 4 adaptive radiance levels for targets of 5 dia. (Fig. 7). Difficulty with conditioning at low-adaptive levels caused the experiments to be terminated at $7 \times 10^{-2}\ \mu W/\overline{cm}^2/\omega$.

The curves for goldfish show similarities to the curves for the human eye (BLACKWELL, 1946). The curves for both sets of data (Fig. 8) have negative slopes. The slope of the curve for the human eye tends to approach zero at the higher adaptive levels. A similar trend might be expected for goldfish if the experiments had been extended to higher levels of adaptation.

At lower adaptive levels the slopes are steeper except for a break at the change from photopic to scotopic vision in the human data. A similar break appears to occur between

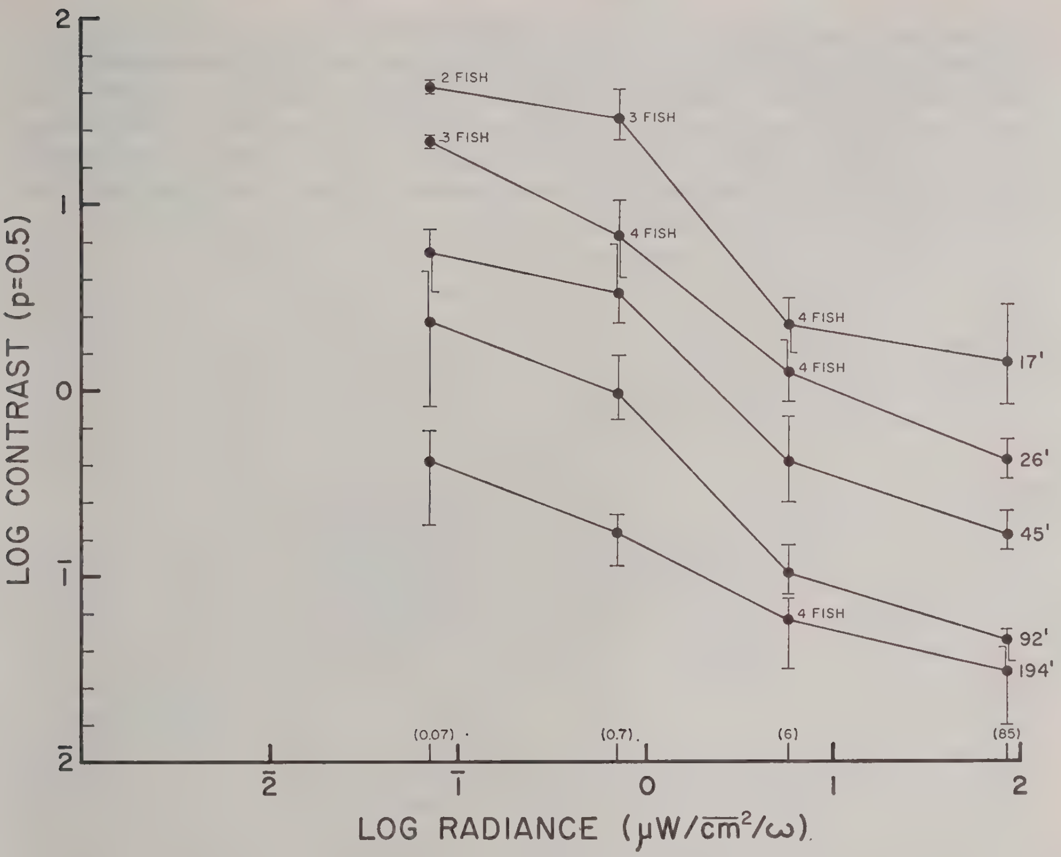


FIG. 7. Relation of contrast threshold to adaptive-radiance for targets of different diameters (17 to 194 min of arc). Points are means for five fish except where specified.

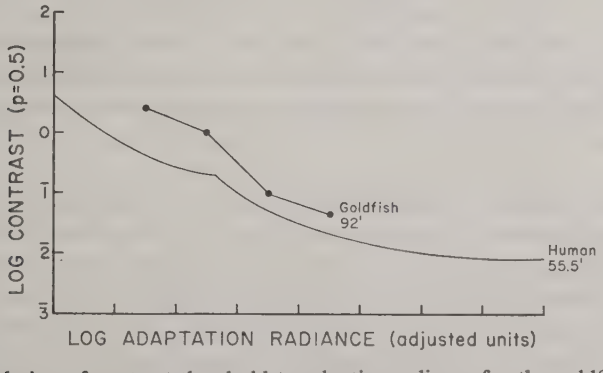


FIG. 8. The relation of contrast threshold to adaptive radiance for the goldfish and for the human eye (after BLACKWELL, 1946). The radiance units have been adjusted to cause the mesopic regions of the two curves to coincide.

1 and 10^{-1} $\mu W/\overline{cm}^2/\omega$ in the goldfish data. Unfortunately, data are lacking for the scotopic portion of the goldfish curves.

Histological examination of eyes from goldfish adapted at 7×10^{-2} $\mu W/\overline{cm}^2/\omega$ shows that some pigment migration had occurred and indicates partial dark adaptation. This level appears to be close to those reported by ALI (1959) for the young of two species of salmon (10^{-1}, 10^{-2} ft-c, about the same as 7×10^{-2} $\mu W/\overline{cm}^2$), although differences in the two experiments render the comparison speculative. Other reports of the mesopic region in fishes (WOODHEAD, 1966) are generally several orders of magnitude lower, but again direct comparisons are impossible.

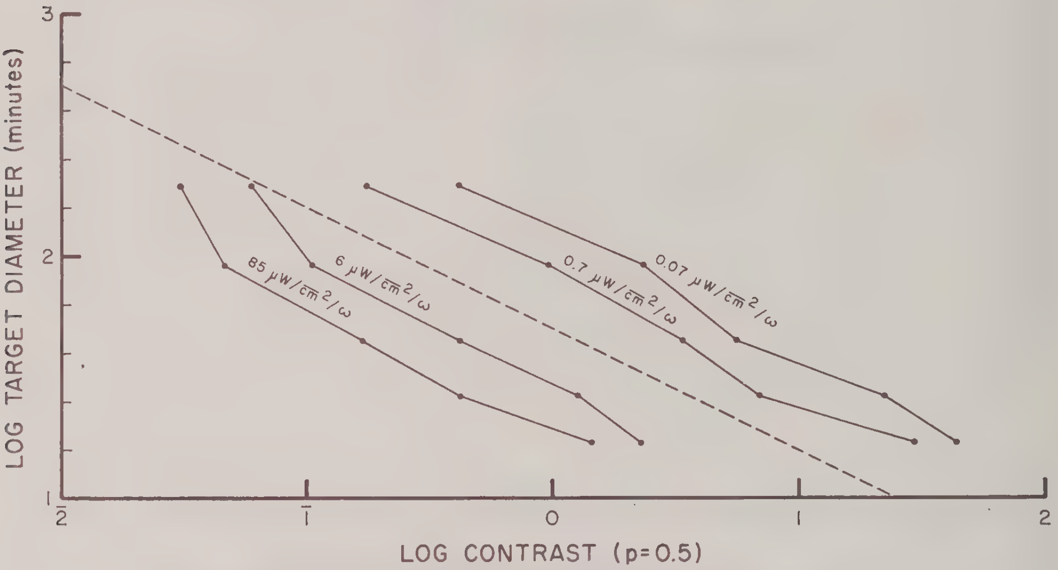


FIG. 9. The relation of target diameter to contrast threshold at each of four levels of adaptive radiance. The dashed line has a slope of —0·5.

The curves obtained when log target diameter is plotted against log contrast threshold (Fig. 9) show several features that are remarkably similar to those in the human data. At high contrasts both sets of data yield curves with slopes very close to —0·5. A slope of —0·5 would be expected if complete summation of the radiant flux occurs regardless of the size of the retinal area covered. Of interest are first that the goldfish data have slopes so near to the —0·5 expected with complete summation; and second that the data do not depart from this slope even for target diameters greater than 100′ of arc (low adaptive levels).

The general interpretation of spatial summation is that a number of receptor elements, rods or cones, are connected into a functional unit, probably in the inner nuclear layer of the retina. The size of these functional units has been postulated to decrease as the retina adapts to higher radiance levels (HECHT, 1928; HECHT and WALD, 1934). Although the mechanisms involved are likely to be more complex than Hecht suggested (PIRENNE, 1962), the general concept has been accepted. Interpreting the goldfish data in terms of Hecht's theory indicates that the size of a functional unit in the goldfish retina must, at any adaptive level, be much greater than that in the human retina.

Hecht originally proposed his theory to explain the relation between acuity and intensity. He later extended the theory to include intensity discrimination. Both acuity and intensity discrimination are special cases of contrast discrimination. One definition of visual acuity is the reciprocal of the minimum separable angle in minutes of arc, when the adaptive state of the eye and the target contrast are specified. The targets usually used are Snellen letters, Landolt's C's, and bar gratings. The target contrast is typically 1·0 and the eye light-adapted. Human visual acuity based on these tests varies from 1·0 to 2·0, corresponding to minimum separable angles of 1·0′ to 0·5′ of arc (WESTHEIMER, 1965). Minimum separable angle has been calculated for a number of species of fish (TAMURA, 1957), on the basis of the separation distance between alternate cones in the retina. In the 27 species examined the smallest calculated minimum separable angle was 4·2′ of arc (0·24 acuity) for *Epinephelus septemfasciatus*. The other 26 species had calculated minimum separable angles which ranged up to 15·4′ of arc (0·065 acuity) for *Chlorophthalmus albatrossis*. Unfortunately, the goldfish was not included in Tamura's study; however, it is possible to calculate minimum separable angle for goldfish by using Tamura's formula and the density of cones for the goldfish eye (Fig. 3). Tamura's formula, based on Matthiessen's ratio, is:

$$\alpha = \frac{1}{F}\left[\frac{0{\cdot}1\,(1+0{\cdot}25)}{\sqrt{n}} \times 2\right]$$

where α = minimum separable angle (radians)
F = focal length of the lens (2·55 × lens radius)
n = maximum number of cones (both single and double) per 0·01 mm^2 of retina (0·1 mm on a side).

The 0·25 is a correction factor for shrinkage and the factor two is to select alternate cones.

For a goldfish having a 2·6 mm dia. lens:

$$F = 3{\cdot}3$$

$$n\ (\text{dorsal/temporal}) = 90 \text{ double and } 30 \text{ single} = 120$$

$$\alpha = \frac{1}{3{\cdot}3}\left(\frac{0{\cdot}25}{11}\right) = 0{\cdot}0138 \text{ radians or } 24' \text{ of arc.}$$

A vertical line at contrast 1·0 (Fig. 9) would be the locus for single-point acuity of the goldfish. Single-point acuity for the highest adaptive radiance is about 0·05 (minimum separable angle, 20′ of arc). This value is amazingly close to the calculated minimum separable angle. The problem of detecting a single point is usually considered as a visual acuity task, but one that is difficult to relate to the tests described previously, namely Snellen letters, Landolt's C's, bar gratings, and retinal measurements. With this difficulty in mind the acuity curve for the goldfish over the range of four adaptive radiances is given in Fig. 10.

For targets which exceed a certain size the relation, threshold × target area = a constant, no longer holds. The slope of the curve changes sharply and becomes asymptotic to the ordinate. This concept of the critical visual angle (BLACKWELL, 1946)—the point at which each curve departs from linearity—is a fundamental property of the eye. One interpretation of this phenomenon that results in a useful generalization is that the threshold is constant for targets subtending angles greater than a certain critical angle. For approximations of sighting ranges this generalization has proven very useful (DUNTLEY, 1963). The critical angle for the goldfish in well-lighted waters is (from Fig. 9) about 100′ of arc and corresponds to a contrast threshold of 0·05.

Relation of contrast threshold to probit slope

The standard deviation (σ) of per cent positive responses about the mean is represented

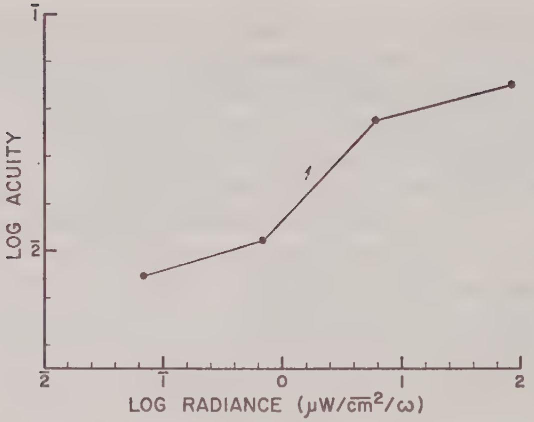


FIG. 10. The relation of single-point acuity to adaptive radiance for the goldfish.

by the reciprocal of the slope of the probit line in probit analysis. In agreement with Crozier's Law, the ratio of σ to the mean $T_{0 \cdot 50}$ is constant. This relation was found to hold for the human eye by BLACKWELL and MCCREADY (1958), where $\sigma/T_{0 \cdot 50} = 0 \cdot 390$ over a range of threshold values of a million to one. The ratio, arithmetic mean $\sigma/T_{0 \cdot 50}$, for goldfish binocular thresholds was 0·585 (S.E. ± 0·0647). Departures from this ratio were not significant in any of the experiments in which binocular vision was tested. The monocular threshold experiments had a mean $\sigma/T_{0 \cdot 50} = 0 \cdot 403$ for targets in the horizontal plane.

Since the binocular threshold data do not show significant departures from a mean $\sigma/T_{0 \cdot 50} = 0 \cdot 585$ regardless of the experimental variable (target size, adaptive radiance, temperature, or fish size), the probit for the normal distribution of per cent positive response and contrast can be used to adjust these data to any other desired detection probability. Values of t corresponding to the desired probability level (Table 1) are to be found in a table of areas of the normal curve of error.

TABLE 1. CORRECTION FACTORS FOR DETECTION LEVELS OTHER THAN 0·50 (NORMAL DISTRIBUTION)

Detection probability	t	$\frac{\sigma \cdot t}{T_{0 \cdot 50}}$	$\frac{T_p}{T_{0 \cdot 50}}$
0·90	1·29	0·75	1·75
0·95	1·65	0·96	1·96
0·99	2·33	1·36	2·36

If the log-normal distribution of the threshold is used instead of the normal, the standard deviation (0·612 for the binocular data) can be considered to be constant regardless of the magnitude of the threshold. For the goldfish data the log-normal distribution gave a smaller χ^2 nearly two-thirds of the time; however, there is little justification for preferring the use of this transformation (BLACKWELL, 1953), and the differences in the thresholds obtained by the two methods were never greater than a few per cent. The values for converting thresholds from log-normal data to some other probability are given in Table 2.

DISCUSSION: THE UNDERWATER VISUAL PROBLEM

DUNTLEY (1963) has shown that for horizontal paths of sight the underwater sighting

TABLE 2. CORRECTION FACTOR FOR DETECTION LEVELS OTHER THAN 0·50 (LOG-NORMAL DISTRIBUTION)

Detection probability	$e^{-t_p \sigma}$
0·90	2·08
0·95	2·74
0·99	4·18

range of a target is determined by the exponential degradation of the inherent target contrast along the path of sight:

$$\frac{C_r}{C_o} = e^{-\alpha r}$$

where C_o = inherent target contrast (measured at the target),
C_r = apparent target contrast (measured at distance r),
e = base for natural logarithms,
α = the spectral volume attenuation coefficient for the water mass,
and r = range to target.

For the light-adapted human eye the contrast threshold $_{(P=0\cdot50)}$ was found to be approximately 0·01 for targets exceeding 15′ of arc in a series of forced-choice temporal method experiments in which binocular viewing, foveal fixation, and a 0·33-sec target duration were used (TAYLOR, 1964). This threshold can be corrected by a series of "field factors" (TAYLOR, 1964) to compensate for unexpected appearance (1·40) and an uncertainty in location of ±4° or more (1·31), and by a confidence-level factor to raise the threshold to the 95 per cent level (1·64). The corrected threshold will be 0·01 × (1·40)(1·31)(1·64), or about 0·032. If this corrected threshold is used in the contrast-reduction formula the underwater sighting range by a swimmer for targets having an inherent contrast of 1·00 would be $\frac{3\cdot5}{\alpha}$ meters when r is measured in meters and α in $\frac{\text{ln}}{\text{m}}$. (The inherent contrast of 1·00 is an absolute value. Dark objects viewed against a light background have inherent contrasts close to −1·00. Such targets are common in the underwater environment.)

The contrast threshold $_{(P=0\cdot50)}$ for a goldfish in well-lighted waters for targets greater than 100′ of arc is about 0·05 (Fig. 9). This threshold was determined by the yes–no rather than the forced-choice method. Thresholds determined by the yes–no method are expected to be slightly greater than thresholds determined by the forced-choice procedure (BLACKWELL, 1953); however, this discrepancy is ignored.

Since the goldfish experiments contained both a temporal and spatial uncertainty factor, corrective field factors have already been applied. To raise the threshold to the 0·95 probability level it must be multiplied by 1·96 (Table 1) to get a corrected threshold $_{P=0\cdot95)}$ of 0·098 and an underwater sighting range $\frac{2\cdot32}{\alpha}$ m.

The fresh water used in the experiments had a spectral volume transmission of 67 per cent/m at 534 mμ; the spectral volume attenuation coefficient is $\alpha_{534}=0\cdot40$. For the goldfish, horizontal sighting ranges of some 6 m would be expected for targets in the binocular field having a contrast 1·0 and an angular subtense greater than 100′ arc. Such a target might be a fat 17 cm black goldfish. Such sighting ranges may seem small when compared with the performance of a human swimmer (8·8 m for a 15′ target), but they are not. The exponential attenuation of contrast tends to minimize any range advantage that might be gained by decreasing the target contrast threshold. The circumstance that threshold becomes asymptotic for targets above a certain size and that this threshold value for goldfish is very close to that for human means that only the smaller critical target-size gains an advantage for the human.

The critical angles of some other fishes are smaller than that of goldfish (TAMURA, 1957; and TAMURA and WISBY, 1963). All of those calculated are smaller than that of the goldfish. This difference would indicate that the critical angles for these fishes are also smaller than the critical angle of the goldfish. On the other hand, the goldfish data show that there is yet little reason to suppose that the contrast-enhancement mechanism postulated by BAYLOR and SHAW (1962) does exist in fishes. Therefore, even though the critical angle is smaller, the contrast threshold of the critical angle may well be the same for all fishes. As an example, the skipjack tuna, *Katsuwonus pelamis*, has a bar grating acuity of about 0·18 (NAKAMURA, 1968)—nearly four times better than the 0·05 single-point acuity of goldfish. Despite the higher resolution of this tuna's optical system, the contrast sensitivity at the critical angle most probably is close to that of the goldfish.

Underwater sighting ranges are much shorter than are the sighting ranges in air. For this reason most targets of interest—predators or navigational aids—will subtend large angles even at the limits of visibility. Smaller objects and food particles are of interest at closer ranges where again the angular subtense will be large. Although the resolution of the fish eye may show manifold differences among species, underwater sighting ranges for large objects (detection) probably are remarkably uniform.

CONCLUSIONS

The goldfish data presented in this paper have implications that probably may be generalized to apply to visual performance in other fishes.

1. Contrast thresholds vary with fish size (lens dia.). The decrease in threshold with increase in size probably may be attributed to the density of the visual elements per unit area of retina, which decreases at a lesser rate than that predicted from the increase in area alone.

2. Contrast threshold is temperature dependent. Visual performance is best at some temperature intermediate between the lower and upper lethal temperatures. For the goldfish this temperature coincides with the temperature of maximum spontaneous activity.

3. Contrast threshold varies with the position of the target in the visual field (retinal position of the image). Threshold is lowest in the binocular field, which is attributed to the increase in probability of detection for binocular vision (binocular threshold is 67 per cent of monocular threshold). For targets in the monocular field thresholds are lower for areas of higher retinal cone density.

4. Contrast threshold varies with target size and the adaptive state of the eye. Targets smaller than a certain critical size are related to contrast in a manner indicative of complete retinal summation. For the dark-adapted eye complete summation is indicated even for targets larger than 200′ of arc. No evidence was found to indicate a special contrast-enhancement mechanism in fishes.

5. The light-adapted goldfish eye has a critical angle (the angular target diameter greater than which contrast threshold does not decrease) of 100′. The critical angle contrast threshold is 0·05, a useful value for calculating underwater sighting ranges. The precision of the experimental determinations of critical angle threshold and binocular contrast thresholds for other target diameters and other adaptive levels are sufficient to permit

the calculation of correction factors for detection levels other than the 0·50 probability level.

6. Acuity is a special case of contrast perception. Single-point acuity for the goldfish interpolated from the experimental data is 0·05 (corresponding to a minimum separable angle of 20′ of arc) for the light-adapted eye. Both acuity and contrast perception show the changes of decreasing adaptive levels characteristic of a duplex retina.

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Abstract—Contrast thresholds of the goldfish eye were determined by the method of constant stimuli using a yes-no conditioned cardiac-response. Computerized probit analysis was used to treat the data. Thresholds were determined for varying temperatures, target sizes, fish sizes, target positions and adaptive radiance levels. Positive contrast, circular targets were used throughout. Both target and adaptive radiance were monochromatic light. Threshold was found to decrease as fish size increased. This change was attributed to the density of cones which decline more slowly as the eye grows than is required to compensate for the calculated expansion of image area in the larger eye. Threshold was found to be temperature dependent, being lowest at 20°C. Threshold was found to vary with the position of the target image on the retina in general agreement with cone topography. Binocular thresholds were lower than monocular thresholds. The relation between target size and contrast threshold was studied at four adaptive levels from a photopic level of 85 μW/cm^2/ω to a near scotopic level of 0·07 μW/cm^2/ω. The data were examined to determine critical visual angle and the region of complete summation. Single-point visual acuity for the goldfish was interpolated from the data. The use of contrast threshold data in underwater visibility

problems is discussed. No evidence was found to indicate a special contrast-enhancement mechanism in fishes.

Résumé—On détermine les seuils de contraste du poisson rouge par une méthode de stimuli constants utilisant une réponse cardiaque conditionnée oui-non. On traitait les données par une analyse électronique. On mesurait les seuils pour diverses températures, dimensions de tests, dimensions de poissons, positions des cibles et niveaux d'adaptation. On utilisait constamment un contraste positif et des tests circulaires. Des lumières monochromatiques étaient employées à la fois pour le test et pour l'adaptation. On trouve que le seuil baisse quand la taille du poisson augmente. On attribue ce changement à la densité des cônes qui, lorsque l'oeil grandit, diminue moins qu'il ne faut pour compenser l'agrandissement calculé de l'image dans l'oeil plus grand. Le seuil dépend de la température, avec un minimum à 20°C. Le seuil varie avec la position de l'image de la cible sur la rétine en accord avec la topographie des cônes. Les seuils binoculaires sont inférieurs aux monoculaires. On étudie la relation entre taille de la cible et seuil de contraste à quatre niveaux d'adaptation, depuis le niveau photopique de 85 μW/cm^2/ω jusqu'à un niveau presque scotopique de 0,07 μW/cm^2/ω. On détermine avec ces résultats l'angle visuel critique et la région de sommation complète. On interpole à partir de ces données l'acuité visuelle du poisson rouge pour un seul point. On discute l'emploi des seuils de contraste dans les problèmes de visibilité dans l'eau. Aucune évidence n'indique de mécanisme spécial pour augmenter le contraste chez les poissons.

Zusammenfassung—Die Kontrastschwellen beim Goldfischauge wurden mittels der Methode des konstanten Reizes bestimmt, wobei eine konditionierte ja-nein-Antwort der Herztätigkeit verwendet wurde. Die Meßwerte wurden durch Probitanalyse mit einem Computer ausgewertet. Die Schwellen wurden für verschiedene Temperaturen, Testgrößen, Testlagen und Adaptationsniveaus bestimmt. Es wurden immer positiver Kontrast und ringförmige Testobjekte verwendet. Adaptations-und Testbeleuchtung waren monochromatisch. Die Schwellen nahmen ab, wenn die Fischgröße zunahm. Die Änderung wurde der Zapfendichte zugeschrieben, die bei wachsender Größe des Auges langsamer abnimmt als notwendig ist, um die berechnete Bildvergrößerung im vergrößerten Auge zu kompensieren. Die Schwelle erwies sich als temperaturabhängig; sie war am niedrigsten bei 20°C. Sie änderte sich auch in Übereinstimmung mit der Netzhauttopographie entsprechend der Lage des Bildes auf der Netzhaut. Die binokularen Schwellen waren niedriger als die monokularen. Der Zusammenhang zwischen Testgröße und Kontrastschwellen wurde für vier verschiedene Adaptationsniveaus, ausgehend von einem photopischen Niveau von 85 μW/cm^2/ω biz zu einem nahen skotopischen Niveau von 0,07 μW/cm^2/ω, untersucht. Die Meßwerte wurden untersucht, um den kritischen Sehwinkel und den Bereich vollständiger Summation zu ermitteln. Aus den Meßwerten wurde die Punktsehschärfe des Goldfischs interpoliert. Die Verwendung von Kontrastschwellen bei Problemen über das Sehen unter Wasser wird diskutiert. Es konnte keine Hinweis auf einen speziellen Kontrast-Verstärkermechanismus bei Fischen gefunden werden.

Резюме — Были определены пороги различения контраста для глаза золотой рыбки методом постоянных раздражителей, с использованием условнорефлекторной «да-нет» сердечной реакции. При оценке результатов был применен «пробит»-анализ с помощью счетно-решающего устройства. Пороги были определены: при разной температуре, разных величинах тестовых объектов, величинах рыб, положениях объектов и уровнях адаптивного облучения. Определялся всегда положительный контраст и объекты были круглыми. Как тестовые объекты, так и адаптивное облучение создавалось монохроматическим светом. Пороги уменьшались пропорционально увеличению размеров рыб. Эти изменения были связаны с плотностью колбочек, которая уменьшается медленнее, когда глаз растет, чем это нужно для компенсации высчитанного расширения области изображения в большем по размерам глазе. Было найдено, что пороги зависят от температуры, они минимальны при 20^0C. Найдено, что пороги изменяются с изменением положения изображения объекта на сетчатке, в общем в согласии с топографией колбочек. Бинокулярные пороги были меньше, чем монокулярные. Соотношение между величиной объекта и пороговым контрастом было изучено на четырех адаптивных уровнях, начиная от фотопического уровня (85 μW/cm^2/ω) и до уровня близкого к скотопическому

(0,07 μW/cm²/ω). Данные были просмотрены с целью определения критического угла зрения и области полной суммации. Отдельные показатели остроты зрения золотой рыбки были интерполированы на основании полученных фактических данных. Обсуждается вопрос об использовании данных о контрастных порогах в проблеме видности под водой. Не было найдено доказательств того, что у рыб имеется специальный механизм усиливающий контраст.

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Artificial Fertilization Among Yellowfin and Gulf Menhaden (*Brevoortia*) and Their Hybrid

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ABSTRACT

Eggs of yellowfin menhaden, *Brevoortia smithi*, were artificially fertilized with sperm from yellowfin menhaden, Gulf menhaden (*B. patronus*), and naturally occurring hybrid menhaden, and reared through the larval yolksac stage at sea under controlled temperature and salinity. Hatching occurred after 38 hours at 21 C. The last larva died 7 days after hatching. Specimens of embryos and larvae were preserved during development and later photographed. Survival of the cross-fertilized eggs equalled that of the intraspecific fertilizations.

INTRODUCTION

Despite extensive investigation of the Nation's valuable menhaden resources (*Brevoortia*: Clupeidae), much is still unknown about the early life history of the various menhaden species. One objective of Bureau of Commercial Fisheries research is to determine more precisely where, when, and how intensively menhaden spawn each year. Studies of the distribution and abundance of the menhaden's planktonic eggs and larvae should yield this knowledge, but these early stages have not been described for all species and their positive identification in biological collections remains a vexing problem in some areas. Early descriptions of Atlantic menhaden (*B. tyrannus*) eggs and yolksac larvae were based on material found in plankton collections. References to these descriptions were listed by Reintjes (1962), who first described eggs and yolksac larvae obtained artificially from the yellowfin menhaden, *B. smithi*. Descriptions are lacking for eggs and larvae of the Gulf menhaden, *B. patronus*, and the finescale menhaden, *B. gunteri*, the former species being of great commercial value in the Gulf of Mexico.

Adding to the difficulty of identifying the planktonic stages of Atlantic, Gulf, and finescale menhaden without the aid of descriptions based on material of known parentage is the problem of identifying the eggs and larvae of menhaden produced by hybridization. Unpublished data collected during two years of exploratory fishing by the Bureau revealed that hybrids make up a substantial portion of the menhaden population along the west coast of Florida between Tampa Bay and Florida Bay. Because many of our plankton collections have been made in areas where hybridization is likely, several questions needed investigation: (1) to what extent are the gametes of sympatric menhaden species interfertile, (2) are the developing hybrid embryos and larvae distinguishable from those produced through intraspecific fertilizations, and (3) are the gametes of naturally occurring hybrids viable?

This paper presents the results of artificially fertilizing eggs of yellowfin menhaden with sperm from Gulf menhaden, yellowfin menhaden, and naturally occurring hybrids of these two species. Mature eggs of the Gulf menhaden or of the hybrids were not available during the experiments, thus reciprocal crosses could not be attempted.

COLLECTION OF RIPE ADULTS

Identification of planktonic fish eggs and larvae entails their comparison with developmental series of eggs and larvae of known parentage. Perhaps the best way to obtain such a series is to fertilize the eggs artificially from mature fish of unquestionable identity and rear the resulting larvae. Monthly cruises of the Bureau's exploratory fishing vessel R/V *George M. Bowers* in the eastern Gulf of Mexico, during the spawning season (November–March), offered opportunities to obtain running-ripe fish.

Monofilament gill nets were used to catch menhaden inside the 20-fathom line between Panama City and Cape Sable, Florida. The nets were set, during daylight, at various depths for one hour at each station. Quick retrieval of the nets yielded fresh specimens with viable eggs and sperm.

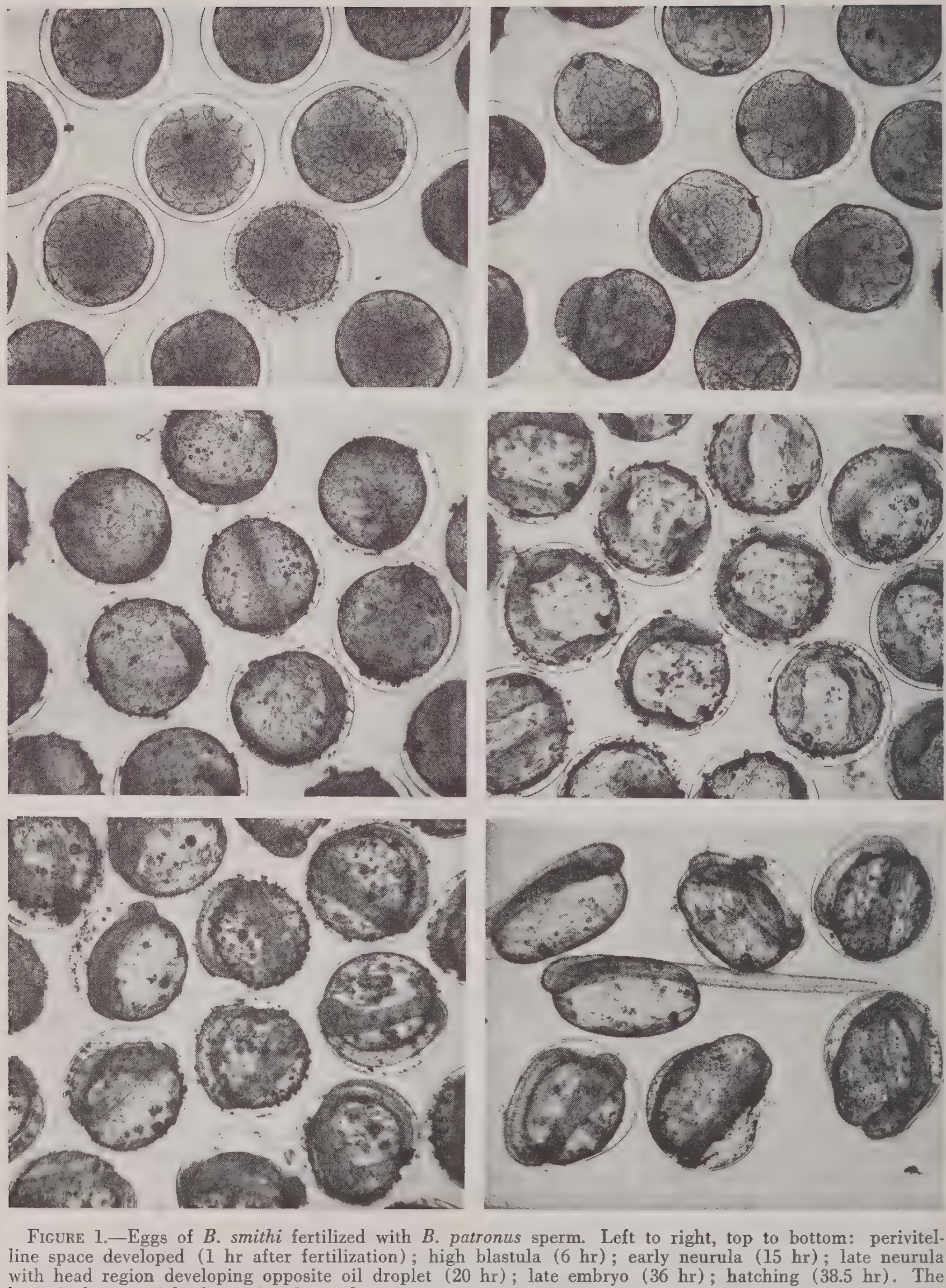

FIGURE 1.—Eggs of *B. smithi* fertilized with *B. patronus* sperm. Left to right, top to bottom: perivitelline space developed (1 hr after fertilization); high blastula (6 hr); early neurula (15 hr); late neurula with head region developing opposite oil droplet (20 hr); late embryo (36 hr); hatching (38.5 hr). The larva in bottom right frame is 3.2 mm long.

TABLE 1.—*Comparison of the seven menhaden used in fertilization trials*

Fertilization group	Species	Sex	Fork length (mm)	Modified predorsal scales	Oblique rows of scales along side	Opercular striae	Margin of pelvic fin	Secondary spots	Frontal groove
I	*B. smithi*	F	224	48	72	weak	oblique	none	none
	B. smithi	M	217	44	73	weak	oblique	none	none
	Hybrid	M	236	41	57	weak	square	none	short
	B. patronus	M	208	32	44	strong	convex	present	long
II	*B. smithi*	F	186	39	68	weak	oblique	none	none
	B. smithi	M	215	46	70	weak	oblique	none	none
	B. patronus	M	226	31	46	strong	convex	none	long

No running-ripe females were caught on six cruises before March 1966, although some females appeared nearly ripe and many males had free-flowing milt. Finally, on the afternoon of 17 March, we collected one ripe female yellowfin menhaden, along with 265 other menhaden 10 miles north of Naples, Florida, in 3 fathoms. Of these fish, 96% were males, most of which were ripe. The predominance of apparent hybrids in this catch (74%), all of which were males, contributed to the unbalanced sex ratio. Seventeen percent of the total catch were Gulf menhaden and 9% were yellowfin menhaden. At this location the water temperature was slightly over 20 C and the salinity was 34‰. The only other ripe female, a smaller yellowfin menhaden, was caught the following afternoon along with 73 other menhaden 1 mile south of Sanibel Island in 2 fathoms of water. Of this catch 80% were males (nearly all ripe); the species composition was 41% hybrids, 5% Gulf menhaden, and 54% yellowfin menhaden. Water temperature and salinity were 23 C and 33‰ respectively.

Each specimen used in the fertilization trials was identified with the aid of descriptions by Hildebrand (1963). The more diagnostic meristic and qualitative characters, including that of the length of the groove above the frontal bones (Dahlberg, 1966), are compared in Table 1.

FERTILIZATION AND REARING

The eggs were fertilized and incubated at sea while the research vessel continued its exploratory cruise. Eggs from the first yellowfin menhaden (Fertilization Group I) were stripped into three dry glass bowls. Several drops of sperm from a male of the same species were mixed with the egg mass in the first bowl. The eggs in the second bowl received sperm from a hybrid, and the eggs in the third bowl were fertilized with sperm from a Gulf menhaden. After 1 to 2 minutes, about 100 ml of filtered sea water were added to each bowl. The eggs, sperm, and water were agitated for the next 5 minutes, and then poured into a 1-liter jar two-thirds full of sea water. The fertilized eggs floated to the surface within 30 minutes and were decanted into additional jars containing sea water. The remaining unfertilized eggs and ovarian tissue were discarded. At this stage, each culture jar contained about 1,500 developing eggs. Eggs from the second ripe female (Fertilization Group II) were stripped into two bowls and fertilized in a similar manner by sperm from a yellowfin menhaden and a Gulf menhaden. Space limitations in the incubator prevented culturing a yellowfin-hybrid cross in this second group. A portable thermostatically controlled refrigerator–heater held the incubation water bath for the rearing jars at 20.5 ± 1.0 C, which corresponded to the temperature of the nearshore Gulf of Mexico. A small air pump kept the water aerated and in motion. When the sea was rough, the jars were removed from the constant-temperature bath, placed in a rack to reduce spillage, and held at room temperature of about 21 C. Part of the water in each jar was replaced twice daily with filtered sea water.

Eggs were sampled and preserved at 1- to 4-hour intervals until hatching. Specimens of larvae were removed every 12 to 24 hours thereafter until the last larva died. Upon absorption of the yolksac, the larvae were fed small plankters and small amounts of finely chopped egg yolk in an attempt to keep them alive. We had no evidence that the larvae fed, however, and all soon died.

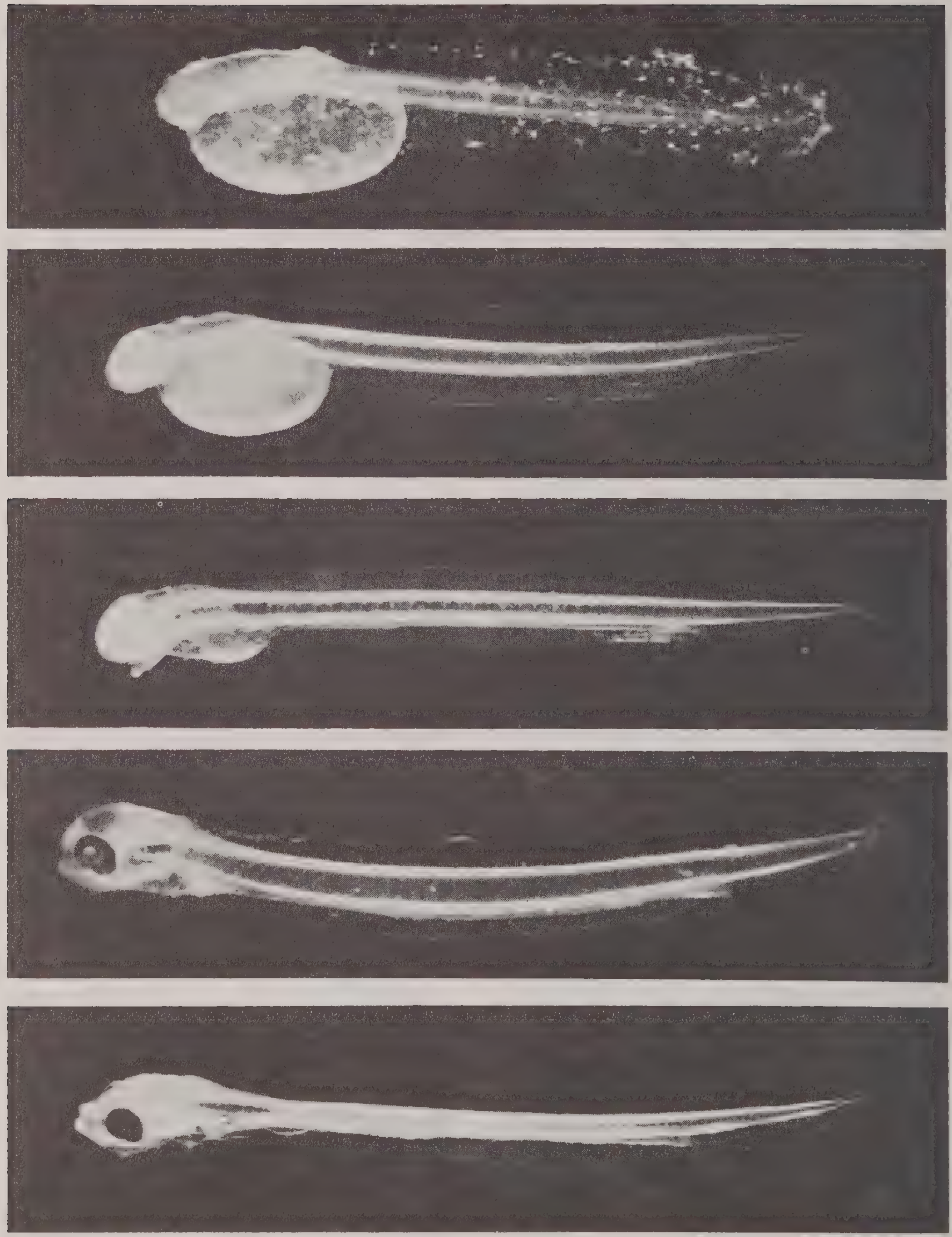

FIGURE 2.—Larvae produced from *B. smithi* female *B. patronus* male. Top to bottom: 3.6 mm (6 hr after hatching); 3.9 mm (26 hr); 4.2 mm (58 hr); 4.5 mm (82 hr); 4.3 mm (130 hr). The eyes became pigmented 70 hours after hatching and the yolk was completely absorbed after 80 hours. The length and thickness of the larvae decreased as is shown in the last frame, this decrease reflecting their failure to feed.

RESULTS OF FERTILIZATIONS

Cross-fertilization of the yellowfin menhaden eggs using sperm from hybrid and Gulf menhaden males produced embryos and larvae visually indistinguishable from those of intraspecific fertilizations. Further, the percentage of eggs that hatched was similar for all fertilizations. Figures 1 and 2 are composite photographs of some stages of one preserved series of yellowfin menhaden eggs fertilized with Gulf menhaden sperm. Direct comparison of these eggs and larvae with preserved eggs and larvae of yellowfin menhaden obtained by Reintjes (1962) from the Indian River in eastern Florida showed that his descriptions of embryo and yolksac larvae development were applicable with the exception of the egg diameter and the ratio of perivitelline space to yolk diameter. Diameters of the fertilized eggs, measured after preservation in 4% neutralized formalin, ranged from 1.05 to 1.18 mm. Their average yolk diameter was 0.98 mm. In comparison, the diameter of eggs artificially fertilized by Reintjes (1962) ranged from 1.15 to 1.30 mm, their average yolk diameter being 0.86 mm. The individual fish's diet, maturity, and spawning history possibly account for the differences in yolk diameter. The smaller amount of perivitelline fluid in the eggs from the Gulf of Mexico may be related to the somewhat higher salinity in which the eggs were fertilized (33–34‰ in the Gulf of Mexico, 26–27‰ in the Atlantic).

Hatching time for the five lots of fertilized eggs reared at 19.5 to 21.5 C was 38 to 39 hours. Hatching time is defined as the time for half of each batch of fertile eggs to hatch. Eggs obtained in similar fashion from yellowfin menhaden along the east Florida coast hatched in 46 hours when held at 18 C, 34 hours at 21 C, and 26 hours at 26 C (John W. Reintjes, personal communication).

SIGNIFICANCE OF FINDINGS

The material and information described in this paper have several practical applications. The developmental series will aid in the identification of planktonic menhaden eggs and larvae, and use of the data on rate of egg development to assign ages to menhaden eggs in biological collections can assist in more accurate location of spawning areas.

The artificial cross-fertilization of yellowfin menhaden eggs with Gulf menhaden sperm showed that the gametes of the species are compatible. The eggs had a hatching potential and the larvae had vigor equal to those of eggs and larvae produced from intraspecific fertilizations of yellowfin menhaden. Since the mature adults of each species occur together during their breeding seasons, natural cross-fertilization and the production of hybrids also are likely. Fish that appeared to be intermediate between the two species were abundant in our catches. The ability of apparent hybrid males to fertilize yellowfin menhaden eggs suggests also that backcrossing is possible. As we observed and as was noted by Dahlberg (1966), less than 1% of all menhaden hybrids were females. The lack of hybrid females would serve as an intrinsic barrier to the production of a self-sustaining population of hybrids and ensure the integrity of the two species.

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THE HAWAIIAN TRAINING PROGRAM FOR TRUST TERRITORY FISHERMEN

by

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THE HAWAIIAN TRAINING PROGRAM* FOR TRUST TERRITORY FISHERMEN

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ABSTRACT

Under terms of an agreement between the High Commissioner of the Trust Territory of the Pacific Islands and the Tuna Boat Owners Association, Honolulu, Hawaii, Micronesians receive on-the-job training aboard the Association's tuna fishing vessels. Trainees receive instruction and practical experience in pole-and-line fishing for skipjack tuna (*Katsuwonus pelamis*) and in gear fabrication, capture and care of baitfish, storage of catches, and vessel maintenance. Thirteen men have completed the 2 to 3 years of training and 24 are in training. The program produces skilled fishermen to man fishing vessels in the Trust Territory.

INTRODUCTION

The Japanese had an intensive pole-and-line fishery for skipjack tuna (*Katsuwonus pelamis*) in the Trust Territory of the Pacific Islands (formerly the Japanese Mandated Islands) prior to World War II. Annual landings fluctuated between 11,700 and 33,100 metric tons during 1935-40 (Shapiro 1948, Table XVII). No commercial fishing for skipjack tuna was conducted in the area after the start of the war. Only recently have U.S. interests begun to develop the fishery. In anticipation of the Trust Territory's having a fleet of its own, the High Commissioner of the Trust Territory sought to have selected Micronesians trained on Hawaiian skipjack tuna fishing vessels in Hawaii.

An agreement was signed between the High Commissioner and the Tuna Boat Owners Association, Honolulu, Hawaii, on 26 February 1962. Under the terms of the agreement, the High Commissioner's Office was responsible for the cost of transporting the trainees. The trainees were to be employed on member vessels of the Association for a maximum of 3 years. Their training could be terminated at any time for medical or personal reasons. They were to be paid 70 per cent of a crew member's share until they qualified for a full share. Their employment was to be terminated if they did not qualify for a full share within 6 months. Throughout their training the Micronesian trainees received only a portion of their earnings each week. The balance was put into a trust fund for them after a fixed amount was sent home each month to take care of their families. When their training was completed the savings of the trainees were turned over to them. In many cases these savings amounted to many thousands of dollars which made the men relatively wealthy at home. Those that have returned home to date have used these funds wisely. Some have improved their homes, one bought an operating copra plantation to take care of his family while he continued to go fishing, several have bought small fishing boats, and four Palauans and four Trukese are drawing up a request for a loan from the government to built two tuna boats, one to be fished in Truk and the other in Palau. Their accumulated savings will make it possible for them to obtain the necessary financial assistance.

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*IPFC/C66/SYM 19.

The trainees were supervised in carrying out the duties of a crew member by the captains of the vessels to which they were assigned by the Association. The trainees received on-the-job training without formal classroom instruction. They were taught techniques of: (1) gear fabrication--rigging fishing poles, making artificial lures, and mending baitfish nets; (2) fishing--hauling-in dummy weights with pole for practice and fishing under the scrutiny of skilled fishermen; (3) baitfishing--participating in night-baiting with a lampara net and day-baiting with a bag net; (4) baitfish care--handling, holding, and feeding of baitfish; (5) storage of catches--handling, stowing, and icing of catches; (6) cooking--grocery purchasing and preparing shipboard meals; (7) vessel maintenance--cleaning, repairing, and stowing of equipment and supplies and hull and deck maintenance.

A new agreement, signed between the High Commissioner and the Association on 21 February 1966, contained two major changes from the 1962 agreement: (1) the trainees were to be employed for a maximum of 2 years; and (2) the Association was to advance the cost of transporting the trainees, but reasonable deductions were to be made from the trainees' wage to repay the Association for the advance.

Under the first agreement, 20 trainees came to Hawaii in 1962 and 14 in 1963; under the new agreement, 18 had come to Hawaii by 1 June 1966. Of the 52 trainees, 13 have completed their training, 24 are still in training, and 15 have returned to the Trust Territory without completing their training. Most of the trainees were from Palau, but some came from Truk, Ponape, and Saipan. The ages of 25 of the most recent arrivals ranged from 19 to 44 years, and averaged about 32 years.

Eight trainees who completed their training in 1965 have returned to the Trust Territory. Since the Trust Territory, until June 1966, was without a skipjack fishing vessel of its own, and since skilled skipjack fishermen are scarce in Hawaii, trainees completing their training in 1966 have been asked by the captains of their training vessels to extend their stay. The trainees are able to comply if the High Commissioner and the U.S. Immigration Service approve. Steps have been taken by the Association to obtain approval.

An official of the Bureau of Commercial Fisheries in Honolulu, Hawaii, was assigned to look after the welfare of the trainees and to make periodic progress reports on the trainees to the High Commissioner.

The program has produced skilled Micronesian fishermen who have returned home to work on the new fishing vessel belonging to the Trust Territory. As additional trainees complete their training in Honolulu they can (1) return to the Trust Territory to work on the government owned and operated tuna boat, (2) pool their savings accumulated while training in Hawaii and purchase a tuna boat and fish on their own, or (3) work on the Van Camp operated fishing vessels now fishing out of Palau. The program has also benefited the Hawaiian skipjack fishery by filling vacancies on undermanned vessels. The Hawaiian fishermen have been pleased with the performance and progress of the trainees and have found them to be reliable and capable of becoming skilled fishermen.

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7. THE DISTRIBUTION AND BIOLOGY OF POLYNEMIDS CAUGHT BY BOTTOM TRAWLING IN INDIAN SEAS BY THE R/V *ANTON BRUUN*, 1963

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Five species, *Polydactylus indicus*, *P. plebeius*, *P. xanthonemus*, *P. sextarius* and *Polynemus paradiseus*, and one subspecies, *P. sextarius* var. *mullani*, of threadfins, family Polynemidae, were caught by bottom trawling in the Bay of Bengal and the Arabian Sea by the research vessel *Anton Bruun* in 1963. The bottom trawling surveys were part of the U.S. Program in Biology of the International Indian Ocean Expedition. The distribution of the threadfins and notes on their size, sex, and stomach contents are presented. Most of the threadfins were smaller than 20 cm. and were caught on the Continental Shelf at depths of 15-122 m. Hermaphroditism was widespread in *Polydactylus sextarius* and *P. sextarius* var. *mullani*, which undergo a protandrous change through a juvenile-hermaphrodite-female series of progressions. Hermaphroditism was also found in *P. plebeius* and *P. xanthonemus*. Crustaceans, especially shrimps, were the most important item in their diet.

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TRAINING PROGRAM FOR SKIPJACK TUNA FISHERMEN IN HAWAII

by

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ABSTRACT

In the response to the need for more fishermen to man the boats of the skipjack tuna fleet, the State of Hawaii in January, 1965, initiated a program in which participants spend 1,950 hours learning the skills requisite for work as commercial fishermen. Most of the training is offered aboard a vessel acquired specially for this purpose. Six students have completed the year's course and are employed in the skipjack tuna fleet. The program is scheduled to last only through 1966 but may be extended.

INTRODUCTION

The annual fish landings for Hawaii in 1950-64 fluctuated between 5.0 and 9.1 million Kg, valued at 2.5 to 4.0 million dollars to the fishermen. There were 2,478 commercial fishermen and 759 commercial fishing vessels in Hawaii in 1950-51**. In 1963-64, the number of fishermen had decreased to 813 and vessels to 373. This decrease was the result of abandonment of the fishing by part-time fishermen because they found it unprofitable. Changes in the age composition of the fishermen during the years are shown by records in Table I for 1950-51, 1958-59, and 1963-64. Although the number of fishermen in each age group and the percentage of young men in the fishery decreased steadily, the percentage of older fishermen remained relatively stable or increased. In 1950-51, 54.8 per cent of the fishermen were 41 years or older and 21.5 per cent were 30 years or younger. In 1963-64, 65.7 per cent were 41 years or older and 12.2 per cent were 30 years or younger.

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*IPFC/C66/SYM 22.

**Statistics on number of vessels and fishermen are given in terms of the fiscal year, which begins July 1 and ends June 30.

TABLE I

THE NUMBER AND PERCENTAGE OF COMMERCIAL FISHERMEN IN HAWAII BY AGE GROUPS IN 1950-51, 1958-59, AND 1963-64

Age	1950-51		1958-59		1963-64	
	Number	Percentage	Number	Percentage	Number	Percentage
<20	128	5.2	33	3.0	17	2.1
21-30	404	16.3	127	11.4	82	10.1
31-40	588	23.7	238	21.4	180	22.1
41-50	792	32.0	283	25.4	222	27.3
51-60	397	16.0	290	26.1	195	24.0
>61	169	6.8	141	12.7	117	14.4
Total	2,478		1,112		813	

Live-bait fishing with pole and line for skipjack tuna (*Katsuwonus pelamis*) is the most important fishery in Hawaii; this fishery contributes 65 to 75 per cent of the weight and 34 to 45 per cent of the value of the annual landings. In 1950, 27 commercial vessels and 280 fishermen were in the Hawaiian skipjack fishery. By 1964, the number of vessels had decreased to 20 (owing mainly to withdrawal of the older vessels from the fishery) and the number of fishermen to 175. Fifteen of the fishermen were Palauan trainees who were in Hawaii to receive 3 years of on-the-job training. Data on the age of 10 of the local fishermen are not available; of the remaining 150, 62 per cent were 41 years or older and 14 per cent 30 years or younger.

Skipjack tuna fishermen earned an average of $4,600 per annum from 1950 to 1964. This amount was small compensation for the long hours of hard work required. Many fishermen and potential fishermen turned to employment ashore to obtain better working conditions and steadier incomes. The skipjack tuna fishery, as well as the other fisheries in Hawaii, is faced with a shortage of skilled fishermen and young recruits to replace retiring fishermen.

The Hawaii training program is directed towards furnishing recruits to maintain and possibly expand the skipjack tuna fishery. The program is funded by the Federal Manpower Development and Training Act of 1962 as amended and is administered jointly by the Hawaii Employment Service of the Department of Labor, and the Manpower Training Section of the Department of Education. The Manpower Training Section of the Division of Vocational and Adult Education, Hawaii Department of

Education, is responsible for the training. Classes are held at the State's Hawaii Technical School in Hilo; shipboard training is conducted aboard the Kula Kai (Hawaiian for "school by the sea"), formerly a commercial skipjack tuna boat, which is berthed in Hilo. The Kula Kai (Fig. 1), purchased by the Department of Education for the training program, has been equipped with an automatic direction finder, ship-to-shore radiophone, loran, radar, and an automatic steering device. The vessel is 24.5 m registered length, weighs 65.3 metric tons, and has a 250-horsepower diesel engine.

SELECTION OF CANDIDATES

The Employment Service of the Hawaii Department of Labor selects the participants. Any unemployed person 16 years or older is eligible. The candidates must be able to float in the water for 5 minutes. They are taken on several short trips on a fishing vessel to see if they are adaptable to work at sea. They must be of stable temperament, so as not to endanger the lives of others, and should be capable of lifting 2.3 to 11.3 Kg weights with a pole and line for periods of 1 to 3 hours. After meeting these requirements, they are referred to the Manpower Training Section as candidates for the program.

FINANCIAL AID

Participants in the program receive varying amounts of financial aid. Unemployed heads of households and bachelors who have had 2 years or more of full-time employment receive training allowances of $40 per week; an additional $5 per dependent per week (but not to exceed $30 weekly) is also included. Transportation allowances may also be provided. These allowances include the cost of public transportation to and from the training facility or payment by mileage. Those who live beyond the commuting area and establish a temporary residence near the training facility receive an allowance of $5 per day. The payment of allowances is authorized after each week of satisfactory performance is certified by the training facility instructor. Some of the participants qualify for additional aid from the Department of Social Services.

TRAINING PROGRAM

The program is now scheduled to continue only through 1966. Results will then be reviewed and the decision made as to whether to continue the program. Each student is expected to complete his training in 1 year. He becomes a member of a section accommodating, at a maximum, 15 or 16 students. A student may enter a section at any time during the school year, but to complete the course must finish the full year of training. The curriculum consists of 1,950 hours of training under 10 main subjects:

Unit	Subject	Hours
I.	Economics of tuna fishing in Hawaii	8
II.	Orientation and familiarization	80
III.	Human relationships	12
IV.	Seamanship	160
V.	Navigation and electronic gear	150
VI.	Methods of propulsion	140
VII.	Hull maintenance	100
VIII.	Cooking	40
IX.	First aid and lifesaving techniques	100
X.	Fishing	1,160
	Total	1,950

The detailed curriculum, as outlined by the Department of Education, is shown in Appendix I. Most of the subjects are taught by the skipper, who is the head instructor, and the chummer and engineer, who are assistant instructors. Another instructor (part-time) is a retired college professor who teaches courses in human relationships and economics. The Fire Department assists in the instruction of lifesaving techniques and scuba diving and the Coast Guard in navigation and chart reading.

PROGRESS AND OUTLOOK

The first section began classes on January 11, 1965, with 15 participants. Only six completed the course and graduated on January 28, 1966. Of the remaining participants, three who did not complete all of their course work will be graduated on June 30, 1966, and six dropped out because they could not adjust to work at sea. The Employment Service placed the six graduates on skipjack tuna vessels, where they are probationary, earning 70 per cent of a share. They will remain on probation until they either prove themselves worthy of a full share by becoming skilled tuna fishermen, or if found incompetent, are asked to leave the fishery. The second section started on November 29, 1965, with 13 new participants and 3 carryover participants from the first section. The job description of a tuna fisherman, as prepared by the Hawaii Department of Labor, is shown in Appendix II.

Most of the participants have been in their teens and twenties, but several were in their thirties and one was 49 years old. He graduated in January and was placed as an engineer, a position in which his age is no drawback. Although it is advantageous to train young men, it is also beneficial to train older men who are potential skippers or engineers since they are hard to locate.

The skipjack fleet is anxiously waiting to receive more graduates from the training program. The Employment Service is finding it very difficult to stimulate participation in the program. Since it would not be justifiable to maintain a training program with only a handful of participants, the success of the program will depend largely upon recruiting and graduating sufficient numbers of men. The effectiveness of the training program in producing well-trained fishermen will have to be evaluated after the graduates have had more time to work in the commercial fleet.

APPENDIX I

Curriculum for the Hawaiian Skipjack Training Program prepared by the Manpower Training Section, Department of Education

Revised - 4/16/64

COURSE OUTLINE

Fisherman, Tuna

Unit I The Economics of Tuna Fishing in Hawaii 8 hours

- A. A perspective
- B. Problems facing the industry
  - 1. Competition from other areas
  - 2. The labor market

Unit II Orientation and Familiarization -- (including shake down cruise on training vessel) 80 hours

Unit III Human Relationship 12 hours

- A. Omnipresent integrant Lab - "What Am I"
- B. Self-evaluation, personality
- C. The other fellow
- D. People are funny
- E. Skill in adjusting
- F. The wholesome personality

Unit IV Seamanship 160 hours

- A. Hawaiian-type sampans
- B. Steering and rudder control
  - 1. Control instruments
  - 2. Steering and rudder control
- C. Anchoring and mooring
  - 1. Anchor handling
  - 2. Securing lines
- D. Towing and transfer at sea
  - 1. The towline
  - 2. Securing and release
- E. Rescue at sea
  - 1. Backing off
  - 2. Assisting vessel
  - 3. Rescue in heavy weather

F. Safety
  1. Gear safety
  2. Fire safety
G. Knots and line
  1. Knot tying technique
  2. Line splicing technique
  3. Types of ropes
H. Skiff operation and maintenance
  1. Maintenance
  2. Hoisting and lowering gear
  3. Outboard motor operation and maintenance
  4. Rowing techniques

Unit V Navigation and Electronic Gear 150 hours
A. Steering by compass
B. Aids to navigation
  1. Buoys
  2. Lights
  3. Range lights
C. Notice to mariners
D. Electronic gear
  1. Radio direction finder (automatic type)
  2. Ship-to-shore radiophone
  3. Radar
  4. Depth recorder
  5. Sonar
  6. Automatic pilot

Unit VI Methods of Propulsion 140 hours
A. Engine types
  1. Diesel
  2. Gasoline
B. Principle of the diesel engine
  1. Definition of diesel
  2. Pressure - temperature relation
  3. Cycle phase
C. Engine maintenance - main engine and auxiliary

Unit VII Hull Maintenance 100 hours
A. Corrosion
B. Painting
C. Dry-docking

Unit VIII Cooking 40 hours
A. Stove operation and maintenance
B. Purchasing and storing of food
C. Sanitation
D. Preparation of balanced meals

Unit IX First Aid and Lifesaving Techniques 100 hours

- A. First aid techniques
- B. Lifesaving techniques in the water
- C. Swimming
- D. Scuba techniques

Unit X Fishing 1,160 hours

- A. Bait catching
    - 1. Surrounding nets
    - 2. Use of attracting lights
    - 3. Use of small skiff
    - 4. Bait tank procedures
    - 5. Care of net
- B. Preparation of fishing gear
    - 1. The bamboo pole -- small and large
        - a. Reinforcements
        - b. Types of line
        - c. Length of line
        - d. Types of hooks
        - e. Securing hooks to line
        - f. Identification
        - g. Care of equipment
- C. Sighting of schools
    - 1. Use of binoculars
    - 2. Observing bird action
        - a. Type of bird
        - b. Behavior of birds
- D. Approaching the schools
- E. Chumming procedures
    - 1. Purpose
    - 2. Quantity chummed
- F. Fishing positions
- G. Techniques in relation to size of fish
- H. Safety precautions
- I. Storage of fish
- J. Cleanup

Total 1,950 hours

APPENDIX II

Job description of a Hawaiian skipjack tuna, pole-and-line fisherman prepared by the Department of Labor

FORM MT-1 (attachment) Page 1

SKIPJACK TUNA FISHERMEN TRAINING PROGRAM

Item 1. Occupation:

a. Description of occupation: Skipjack, Pole-and-Line Fisherman

1. Fishes for skipjack (tuna) on the high seas, works as a team member of a crew of 10 to 12 fishermen on large (75 to 95 ft.) boat. Mans assigned station after tuna school is spotted and lured near craft. Pulls in fish using bamboo pole and hook; may work in team of two or three men to haul in larger fish.

2. May assist in chumming operations.

3. Catches bait using nets, handles operation of bait skiff, prepares bait tanks for proper storage of bait; repairs bait nets.

4. Prepares, maintains and uses fishing gear, such as bamboo poles, lines, hooks, and other gear as required.

5. Participates in unloading catch from vessel to dock.

6. Performs cleanup operations of craft and gear.

7. Assist in locating schools of fish by use of binoculars and electronic equipment.

8. Identify navigational aids for the safety of the crew and vessel.

9. Operate direction finder, ship-to-shore radiophone, radar when available, depth recorders, sonar and automatic pilot.

10. Participate in rescue work when necessary; may operate skiffs; stands wheel watches at sea; participates in anchoring and mooring of vessel.

11. Assists in maintenance and repair of diesel and gas engines, hull and superstructure.

12. Acts as cook--purchases and stores food, prepares balanced meals, and maintains cooking equipment and ares in sanitary condition.

b. Training objective: To develop skills that will enable workers to be fishermen (entry level) initially and journeymen within a reasonable period. Training should be for Skipjack, Pole-and-Line Fisherman. The specific skills required are identified in the description of the occupation as per item la above. Industry representative will continue training after employment. This training must include elements concerning the maintenance and operation of a fishing craft and its equipment. Emphasis will be to train the worker to be a member of a team of which each crewman is an integral part.

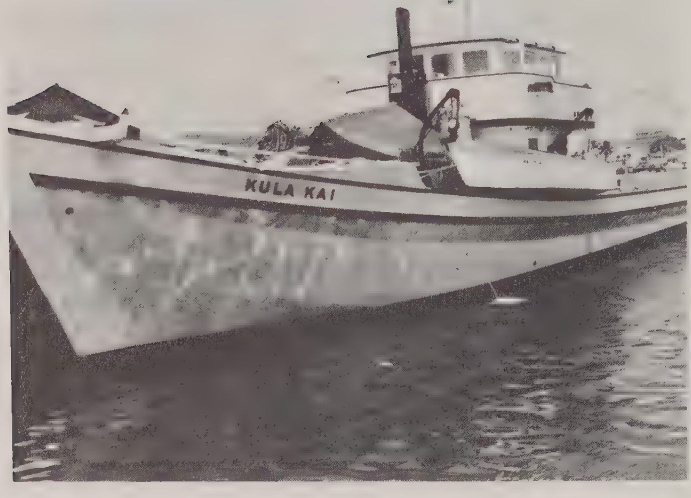

Fig. 1. The Kula Kai, formerly a commercial fishing vessel, is used by the State of Hawaii in its program for training fishermen for the Hawaiian skipjack tuna fleet.

Proceedings of the National Shellfisheries Association
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VITAL STAINING OF BIVALVE MOLLUSK SHELLS WITH ALIZARIN SODIUM MONOSULFONATE

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ABSTRACT

Alizarin sodium monosulfonate was used for vital staining of shells of larval and post-metamorphic hard- and soft-shelled clams, Mercenaria mercenaria *and* Mya arenaria. *In post-metamorphic clams a week-long immersion in 5 to 20 ppm alizarin resulted in peripheral and medial deposition of red shell material. Larval* M. mercenaria, *when subjected to 0.25 to 0.75 ppm alizarin for 48 hours, produced distinctive check marks on shells which may have value in marking. The long persistence (at least 18 months in the present study) of metabolically induced red shell coloration gives this method an advantage over more superficial marking techniques used in ecological research.*

INTRODUCTION

Shells of living mollusks have been marked for later identification in various scientific studies by painting (Carriker, 1955), tagging (Posgay, 1961), notching (Rounsefell, 1963), and application of fluorescent material (Tufts, 1967). Larvae of pelecypods have been marked by staining the soft tissue with neutral red (Loosanoff and Davis, 1947). These methods have been successful for their purpose to greater or lesser degree but all have disadvantages that limit their general applicability. Most require the handling of individuals, which precludes marking the great number of animals which are often necessary to obtain meaningful ecological data. A method such as painting may produce ephemeral marks or may cause mortality through injury, limiting its usefulness in studies requiring identification of marked individuals after a time lapse.

Alizarin sodium monosulfonate has been used in vital staining of vertebrate bone (Lillie, 1952). Also, Turner[2] used alizarin dye in marking the calcareous tubes of the marine polychaete *Hydroides dianthus*. These applications suggested that alizarin might also be used as a vital stain for the shells of bivalve mollusks.

The experiments reported here demonstrate the incorporation of alizarin red coloration in the deposition of new shell material in post-metamorphic hard- and soft-shelled clams, *Mercenaria mercenaria* and *Mya arenaria.* Also, alizarin has produced distinctive check marks on shells of larval hard-shelled clams.

MARKING POST-LARVAL BIVALVES

In the initial trials, post-metamorphic *M. mercenaria* were successfully marked by holding them in a solution of alizarin in sea water. Clams 2 to 3 mm in width across the shell were produced in the hatchery by spawning and rearing techniques summarized by Loosanoff and Davis (1963). One hundred clams were placed in each of several glass 1-liter beakers containing concentrations of alizarin of 0.25 to 20 ppm. Other beakers contained untreated animals as a control. All were reared for 7 days at 24° C in sea water that had been filtered and treated with ultra-violet light; the water and the alizarin concentrations were renewed at 2-day intervals. A mixture of live flagellates, *Isochrysis galbana, Dunaliella euchlora, Mono-*

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chrysis lutheri, and *Chlorella* 580, was fed every day at an approximate rate of 0.01 ml of packed cell volume per liter culture per day (Davis and Guillard, 1958).

Clams were active and feeding at all test concentrations of alizarin during the treatments. Shell exteriors soon became stained uniformly dark red.

After treatment, clams were held in screened cages in Milford Harbor for later observation. Under outdoor summer conditions all clams grew rapidly and soon lost the general dark red coloration of alizarin. The red margins of the shells, however, representing areas of growth during alizarin treatment were retained as red bands and had faded very little up to 18 months after treatment (Figures 1 and 2 show alizarin marks 6 months after treatment). The red bands were most distinctive at the higher dosage rates of alizarin, between 5 and 20 ppm, and appeared to be excellent marks.

In an attempt to place more than one red band on a single clam, the clams of the original experiment were subjected to a second 7-day exposure of alizarin (8 ppm in this trial) after a month's post-marking growth in the natural environment. The clams again acquired general dark red coloration. When returned to natural conditions the red color again faded, but a second red band was formed representing shell growth during exposure to the second alizarin dosage (Figs. 1 and 2).

Results of trials with *M. arenaria* were equally good. Juvenille *M. arenaria* were subjected to a 7-day treatment with 5 ppm of alizarin under conditions described above and then held under natural conditions for observation. Six months after treatment these clams had added new shell and had also retained red bands on the shells (Fig. 4). In addition to the persistent red bands, the general red coloration of the shell had not faded to normal coloration, but has remained light pink (Fig. 4). The pink shell, contrasting with the white color of shell deposited later also produced a distinctive marking effect. Similar results were obtained with the coot clam, *Mulinia lateralis.*

Cross-sections were made of shells to determine the site of alizarin deposition. Sections of *M. mercenaria* shells marked with a single red band revealed a red striation running with the laminae and extending through the complete thickness of the shell (Fig. 3). Sections of *M. arenaria* shells showed that the red coloration was deposited on the entire inner surface of the shell and extended to the outer surface in the area which was peripheral at the time of treatment (Fig. 5). Colorless shell beneath the red band represents additional medial shell that was deposited when clams were returned to natural conditions.

MARKING LARVAL BIVALVES

Larval *M. mercenaria*, when exposed to alizarin, produced a distinctive check mark on the shell. The larvae, like the post-larval animals, were initially treated for 7-day periods. Concentrations of alizarin below 0.10 ppm produced no ill effects or distinctive marking; concentrations higher than 0.25 ppm stopped growth and produced high mortality. If, however, larvae were subjected to 0.25 to 0.75 ppm alizarin for 48 hours and then returned to untreated sea water, growth of larvae

FIG. 1 and 2: *External and internal shell surfaces of alizarin-marked juvenile* M. mercenaria, *6 months after marking. The smaller clam at right shows single red band after one 7-day alizarin immersion (5 ppm) whereas the larger individual at left shows two bands that represent two separate marking treatments; size bears no relationship to treatment. Shell length parallel to hinge line of largest individual — 6 mm.*

FIG. 3: *Cross-section of shell perpendicular to hinge line of juvenile* M. mercenaria *which received single alizarin treatment 6 months before sacrifice. Red striation reveals site of shell deposition during term of alizarin immersion. Shell length parallel to hinge line — 11 mm.*

FIG. 4: *External shell surface of alizarin-marked juvenile* M. arenaria *6 months after marking. Visible is red band and general red discoloration of the shell representing alizarin deposition with peripheral and medial shell growth during the term of alizarin treatment. Shell length parallel to hinge line — 2 cm.*

FIG. 5: *Cross-section perpendicular to hinge line of juvenile* M. arenaria *which received single alizarin treatment 6 months prior to sacrifice. Red striation reveals site of shell deposition during term of alizarin immersion. Shell length parallel to hinge line — 2 cm.*

FIG. 6: *Late stage larval* M. mercenaria *showing check marks produced by 48-hour immersion in 0.40 ppm alizarin. These shell marks are distinct from a later demarcation line between the prodissoconch shell of the larva and the dissoconch shell of the metamorphosed individual. Shell length parallel to hinge line — about 200 μ.*

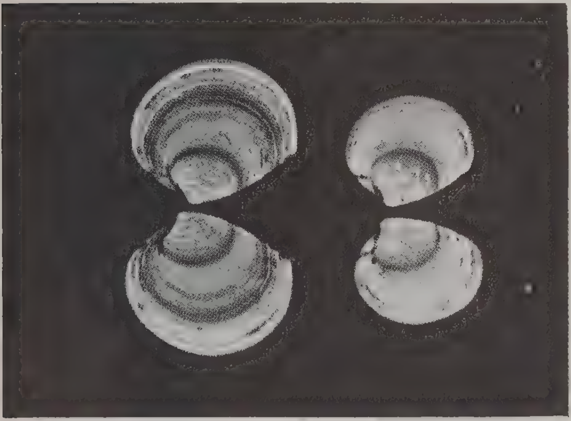

FIG. 1

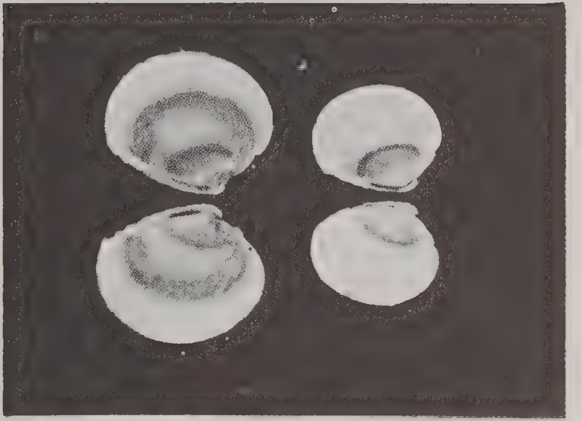

FIG. 2

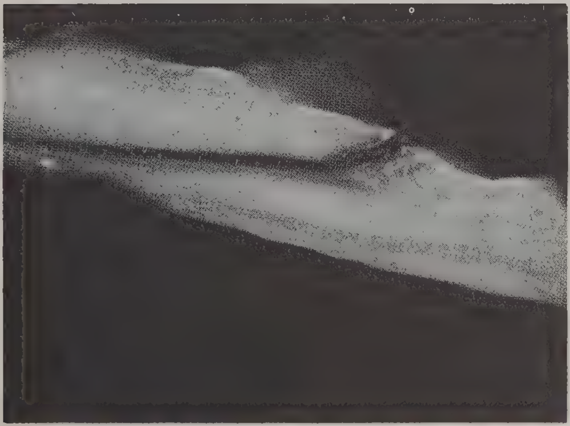

FIG. 3

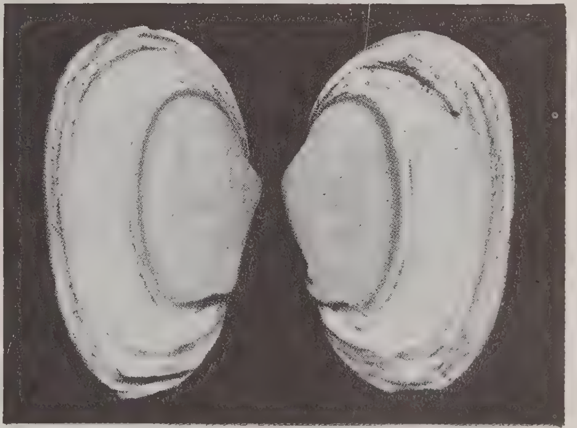

FIG. 4

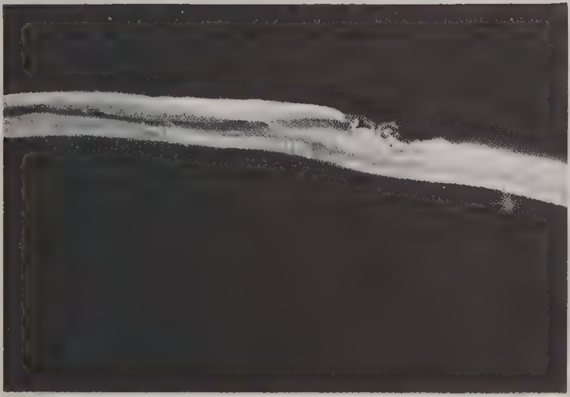

FIG. 5

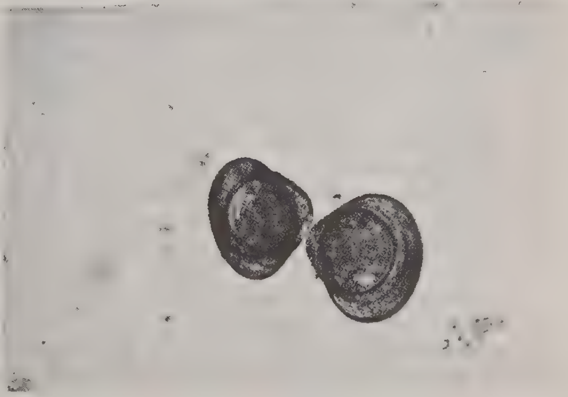

FIG. 6

resumed and a very distinctive check mark resulted (Fig. 6). Immersion in 0.30 to 0.40 ppm for 48 hours produced a light check mark recognizable in all individuals. With increasing concentrations check marks became more pronounced, until at 0.75 ppm larvae greatly indented the shell before normal growth was resumed. Larvae subjected for 48 hours to concentrations of alizarin above 0.75 ppm were unable to resume normal growth.

M. mercenaria larvae of all sizes from 115 μ straight-hinge veligers up to 225 μ pediveligers were marked in this manner, although success was somewhat more difficult to achieve than in the technique used for post-larval clams. Many cultures of marked clam larvae were reared past metamorphosis; the check marks could be readily identified as long as the larval shell itself was recognizable in the juveniles. Considerable work remains in testing the general value of this method of marking, but it probably could be used for marking other species as well.

DISCUSSION

The red bands in post-larval shells of *M. mercenaria* and the bands and pink discoloration of *M. arenaria* appear to result from the deposition of alizarin in the new shell added during treatment. The deposition of red shell was first suggested by the rapid fading of red coloration in all areas of the shell except in the area which was peripheral during the exposure to alizarin. Later, cross-sections of shells (Figs. 3 and 5) revealed sharp alizarin bands only on shell surfaces which were medial and peripheral during time of treatment.

An adequate food supply favoring shell deposition during alizarin treatment would appear to be the determining factor in the laying down of a distinctive mark, although present experiments have not conclusively demonstrated this. Adequate food may be particulary important in marking smaller juvenile animals because their growth rates may depend more on immediate food supply than on a stored food reserve (which might be more important for larger, more mature mollusks).

The alizarin marking method will be useful in ecological research requiring the marking of a large number of shellfish with a highly durable mark. The only limitations on the number of individuals that can be marked are the ability to keep them under such conditions that adequate shell deposit is formed while the animals are being treated and the number of animals that can be procured either through collection of wild stock or through hatchery rearing. Marks appear to be stable and are expected to persist for the life of the animal. After 18 months the marks had faded very little.

Certain difficulties might be expected in the field use of the alizarin technique. Marked animals released in natural water undoubtedly will become dark or discolored, thus obscuring the mark on the shell exterior. It may be necessary to hold the captured animals in sea water away from a substrate for several days to bleach shells sufficiently to distinguish marked individuals. Alternatively, shells of live mollusks could be filed lightly for examination of subsurface shell for traces of red marking. If the animals were to be sacrificed, the interior margins or complete cross-sections of shells could be examined.

M. mercenaria shells on occasion contain natural purple striae which might be mistaken for an alizarin mark. Nearly all natural striations of this type instead of running the complete thickness of the shell are confined to the medial third of the shell. The natural striae are probably variations of natural purple pigmentation of certain areas of the inner translucent region (Shuster, 1957), and seem to be associated with less than optimum growth conditions in *M. mercenaria*. Such coloration has not been observed in *M. arenaria*.

Trials are being continued to determine the general applicability and limitations of the method in molluscan research. No doubt other species of pelecypods and also gastropods can be similarly marked.

ACKNOWLEDGMENT

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Description of Laboratory-Reared Larvae of *Paralithodes platypus* (Decapoda, Anomura, Lithodidae)[1]

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ABSTRACT

Larvae of the blue king crab, *Paralithodes platypus* (Brandt), were hatched and reared in the laboratory. All larval stages obtained developed in a manner similar to the development reported for other lithodid anomurans. In culture, *P. platypus* had four zoeal stages and a single glaucothoeal stage. The feature which distinguishes all zoeal stages of this species from zoeae of the other two North Pacific species of *Paralithodes* — *P. camtschatica* and *P. brevipes* — is the presence of 9 + 9 telson processes (including a hair-like second process) rather than 8 + 8 telson processes. Glaucothoes of *P. platypus* have one more pair of spines in the branchial region of the carapace than do those of *P. camtschatica*. Glaucothoes of *P. ptatypus* have 15 pairs of spines on the dorsal surface of the carapace, not including the spines of the frontal area (rostral complex) or the suborbital spines, whereas glaucothoes of *P. camtschatica* have 14 pairs of spines, and those of *P. brevipes* have 13 pairs.

INTRODUCTION

Paralithodes platypus (Brandt), called the blue king crab in Alaska, is an anomuran crustacean of the family Lithodidae. The genus *Paralithodes* has five species, three of which — *P. camtschatica*, *P. brevipes*, and *P. platypus* — have broadly overlapping distributions in the northern half of the North Pacific Ocean. In the west, the range of *P. platypus* extends from the coast of Hokkaido, Japan, northward along the eastern shores of the Kamchatka Peninsula and into the southern Bering Sea (Makarov, 1938). Farther east this species is found south of the Aleutian Islands, around Kodiak Island, and along the coast of the Gulf of Alaska. The most southerly point of its distribution on the eastern Pacific coast appears to be Gambier Bay on Admiralty Island in southeastern Alaska (57°27′N lat, 133°53′W long) (Carl Lehman, Alaska Department of Fish and Game, personal communication).

The most comprehensive review of the literature on the larval development of lithodid crabs appears in Hart's (1965) paper describing the life history and larval development of *Cryptolithodes typicus*. Hart's review does not include the nearly concurrent publication by Kurata (1964) of a comprehensive description of the developmental stages of lithodid larvae of Hokkaido, Japan, including a key for their identification. Kurata described the first zoeal stage of *P. platypus* and all the larval stages of *P. camtschatica* and *P. brevipes*.

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Of the three species of *Paralithodes* found in the northern part of the North Pacific, two — *P. camtschatica* and *P. brevipes* — have been reared in the laboratory through all of their larval stages. The first complete description the larval stages of *P. camtschatica* was by Marukawa (1933). The source of zoeal stages I and II was eggs hatched in the laboratory, and that of later stages was the plankton. Sato (1958) also discussed the development of larvae of *P. camtschatica*. Experimental work on the larvae of this species was carried out by Kurata. He studied rearing techniques, kinds of organisms eaten and the rate of their consumption by king crab larvae (Kurata, 1959, 1960a), and the effect of temperature and salinity on growth and survival of larvae (Kurata, 1960b). A larva intermediate between the normal last zoea and the glaucothoe was described for *P. camtschatica* and *P. brevipes* from specimens reared in the laboratory (Kurata, 1960c). Kurata (1956) reared *P. brevipes* and found that this species has only three zoeal stages instead of the four formerly assumed to characterize the genus. Both *P. camtschatica* and *P. brevipes* have a single glaucothoeal stage, as do all lithodids described to date (Sato, 1958; Kurata, 1964; Hart, 1965).

Larvae of *P. platypus* have been the least thoroughly described. Marukawa (1933) illustrated the first zoeal stage but because he made no mention of rearing these larvae, it is assumed that they were taken from the plankton. Sato (1958) illustrated zoeal stages I–IV but gave no detailed descriptions. The illustration of the first zoeal stage was based on Marukawa's work, and those of stages II–IV were made from individuals collected from the intestinal tract of juvenile pink salmon. Thus, the source of Sato's material was not larvae reared in culture as Hart (1965) had assumed. Kurata (1964) described stage I zoeae taken from the plankton. This larval stage was the only one that he obtained. Kurata briefly discussed stages II–IV, basing his comments on Sato's (1958) work.

Because of their importance, I obtained English translations of the relevant parts of the papers by Sato (1958) and Kurata (1964) and for all of Marukawa (1933). I used only the English summaries and the illustrations in the other Japanese papers cited.

The previous descriptions of morphology of the larval stages of *P. platypus* were based on specimens from the plankton and the contents of pink salmon stomachs. Species identity could not be known positively. In the present study a gravid female *P. platypus* with hatching eggs was brought into the laboratory where the larvae were collected and reared. The resulting four zoeal and single glaucothoeal stages are described.

The larvae reared during this study were sent to Dr J. F. L. Hart of Victoria, B.C., for final disposition in the British Columbia Provincial Museum.

METHODS AND MATERIALS

On April 7, 1965, I captured a clasping pair of *P. platypus* while I was skin diving in Auke Bay, Alaska (58°21′N lat, 134°14′W long). The female was ovigerous, and the eggs were hatching. The length of her carapace was

149.5 mm from the posterior margin of the right orbit to the posterior medial margin of the carapace, and the width was 161.5 mm across the widest part of the carapace, not including the spines.

Zoeae were obtained and cultured in the following manner. The gravid female was held in a large aquarium with continuous running sea water. The eggs were allowed to hatch naturally, which precluded observing prezoeae. The first zoeae were removed from the aquarium with a large-bore pipette and placed in glass finger bowls (5 mm deep × 8 mm in diam). Initially six zoeae were placed in each bowl. Additional larvae for preservation at various stages were kept in large glass beakers. The larvae in the finger bowls were examined daily, and signs of molting, disease, or death were recorded. The duration of the larval stages was determined from these observations.

Nauplii of brine shrimp (*Artemia* sp.) were added to the bowls daily as food for the larvae. In addition, the glaucothoes also received small amounts of minced clams, *Protothaca* sp., on which they appeared to feed.

The water used in this study was taken from the natural environment. The static water in the culture bowls was changed every second day. The culture dishes were kept in a circulating seawater bath whose temperature increased gradually from 4.5 to 7.2 C (40.1–45.0 F) during the $2\frac{1}{2}$-month study. The increase in temperature of the bath water corresponded to the seasonal increase in temperature of the bay from which the sea water was taken. The salinity of the cultures varied between 30.0 and 32.0‰.

Drawings of appendages were made from exuviae from the finger bowls, and drawings of whole animals were made from preserved specimens from the mass cultures in the beakers. All illustrations were prepared with the aid of a camera lucida. The left appendage was drawn unless stated otherwise. When setae were plumose, the fact is noted in the text but usually is not shown in the drawings. This omission made it possible to show other details. Exuviae and preserved animals were cleared in lactic acid and were drawn while immersed in this medium (Humes and Gooding, 1964).

An ocular micrometer was used to measure body dimensions of the larvae — carapace length, total body length, and total carapace length. *Carapace length* is the straight-line distance from the posterior margin of the orbit to the mid-dorsal posterior margin of the carapace. Carapace length is the standard measurement in this study because it is the least subject to variations caused by preservation and handling and also because it is generally used in studies of juvenile and adult crabs. *Total body length* is the distance from the tip of the rostrum to the posterior margin of the telson, not including the telson processes. An accurate measurement of total body length is difficult to obtain in preserved larvae because the abdomen is generally flexed tightly beneath the carapace. This measurement requires the summation of several straight-line measurements or chords of the arch formed by the dorsal margin of the body. *Total carapace length* of the zoea is the straight-line distance from the tip of the rostrum to the tip of the lateral spine. In the glaucothoe, total carapace length is measured from the tip of the rostrum to the posterior mid-dorsal margin because of a change in the form of the carapace. Data on average total body length and total carapace length are presented to facilitate comparison with similar measurements given in the literature. The *width of the carapace* of the glaucothoe is the distance across the widest part of the branchial region between spines.

Nomenclature of the larval appendages follows that of Gurney (1942), except when noted. The term "telson process," proposed by Pike and Williamson (1960), includes spines, setae, or hairs on the telson. The setation formula of the endopodite is the numbers of setae per segment from the distal to the proximal segment.

GENERAL REARING DATA

Forty-eight stage I zoeae were placed in glass bowls (six per bowl). Table I shows the number of individuals surviving to the beginning of each larval stage, the duration of each stage, and the accumulated mortality (expressed as the percentage of the original larvae that had died by the end of each larval stage). Mortality was greatest late in zoeal stage I, when some individuals died apparently without starting ecdysis and others without completing ecdysis or exuviation.

TABLE I. Duration of the larval stages (days) and cumulative mortality (per cent) through each stage of *Paralithodes platypus* reared in the laboratory.

Larval stage	Larvae entering each stage	Duration		Cumulative mortality through each stage
		Avg	Range	
Zoea I	48	12.4	10–15	75
Zoea II	12	12.3	11–14	77.1
Zoea III	11	12.5	11–15	83.3
Zoea IV	8	14.3	13–17	87.5
Glaucothoe	6	12.8[a]	9–18[b]	100
Post-larvae	0	–	–	–

[a]No glaucothoes molted to the first post-larval stage. Since most of the deaths of the larvae occurred just before ecdysis, the date of death was assumed to be the date of ecdysis.

[b]The range is the number of days the glaucothoe lived.

Under the conditions of this study, *P. platypus* went through four zoeal stages and molted into the glaucothoeal stage. None of the glaucothoes molted to the post-larval stage. It is assumed that *P. platypus* has a single glaucothoeal stage, as in all other species of Lithodidae described to date.

DESCRIPTIONS OF LARVAL STAGES

STAGE I ZOEA

The average carapace length (from eye notch to mid-dorsal margin of carapace) of stage I zoeae (Fig. 1*a*) is 1.2 mm (42 specimens); the average total carapace length (from tip of rostrum to tip of lateral spine) is 3.2 mm (10 specimens); and the average total body length (from tip of

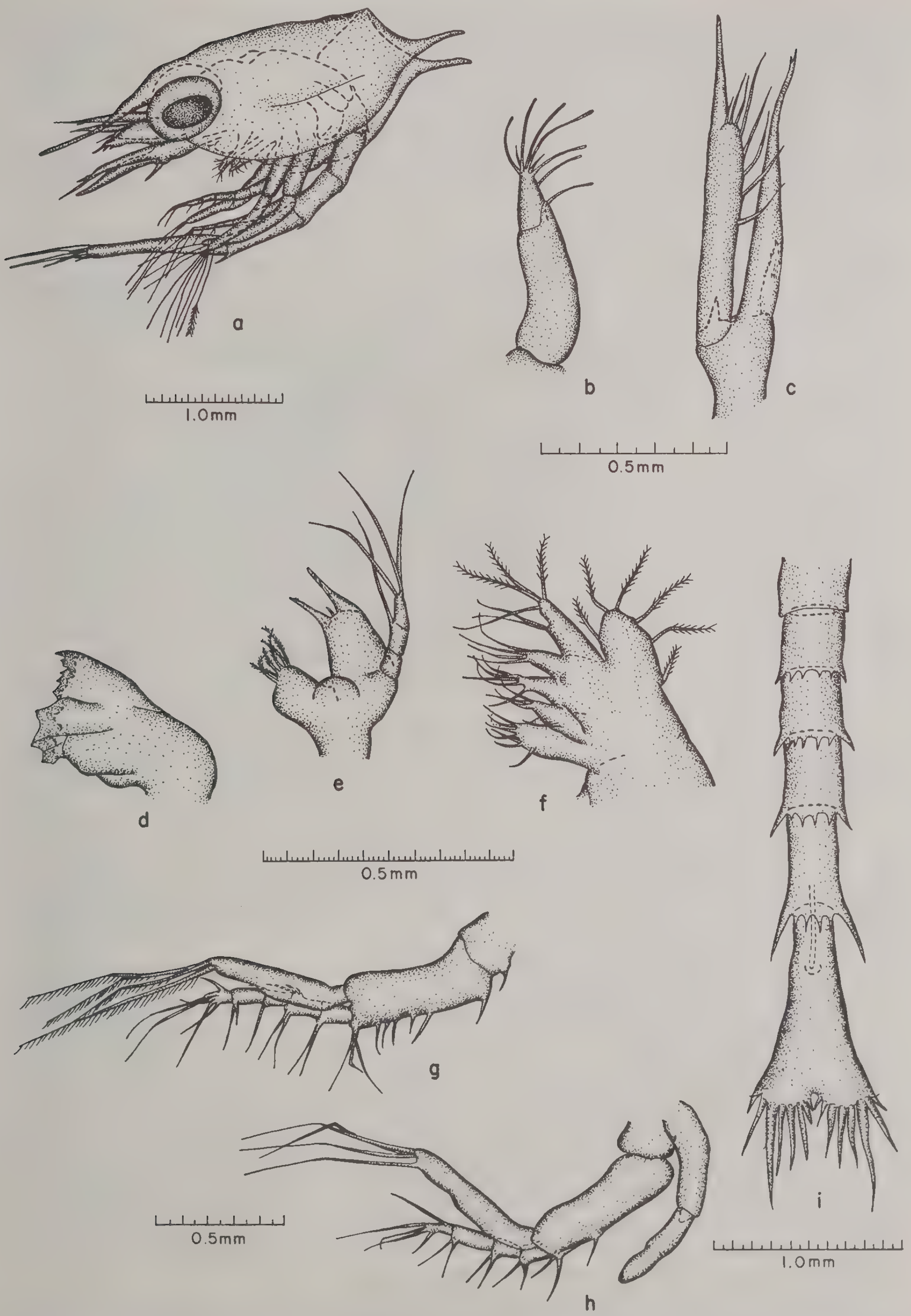
a
1.0mm
b
c
0.5mm
d
e
f
0.5mm
g
i
0.5mm
1.0mm
h

FIG. 1. (*a*) Stage I zoea of *Paralithodes platypus*; (*b*) antennule; (*c*) antenna; (*d*) mandible, right; (*e*) maxillule, right; (*f*) maxilla, right; (*g*) first maxilliped; (*h*) second and third maxillipeds; (*i*) abdomen and telson.

rostrum to posterior margin of telson, not including telson processes) is 4.9 mm (7 specimens). Lateral carinae extend toward the spines on the postero-lateral margin of the carapace and are present in all zoeal stages. In all zoeal stages the carapace has a slight medial crest, which bears a noticeable hump at the base of the rostrum, and the rostrum is approximately one-third the total carapace length. The eyes are sessile in stage I only.

Antennule (*Fig. 1b*). — The outer distal segment of the antennule has seven aesthetes and two small setae. The proximal segment has no setae, although this segment has an extension or distal lobe on the medial side. This lobe is slightly more than one-third and less than one-half the length of the distal segment.

Antenna (*Fig. 1c*). — The antenna has a basal segment which bears two stout spines. The medial spine is segmented from the basis, and the distal half is denticulate. The lateral spine is smaller and smooth and is not segmented from the basal segment. The exopodite (antennal scale) has eight sparsely plumose setae on the medial margin and terminates in a long slender projection which extends beyond the end of the endopodite. The narrow endopodite is not segmented from the basis and terminates in a finely bifid tip. The exopodite and endopodite are subequal in length in all zoeal stages.

Mandible (*Fig. 1d, right mandible*). — The mandible has a series of small teeth dorsally and larger teeth on the molar process. There is no indication of a mandibular palp in any zoeal stage.

Maxillule (Fig. *1e, right maxillule*). — The endopodite (palp of Hart, 1965) is three-segmented; it has three setae on the terminal segment, one on the middle segment, and none on the basal segment. The distal end of the basal endite has two short spines and two large spines; each of the latter bears a row of spinules. The proximal coxal endite has six sparsely plumose setae.

Maxilla (*Fig. 1f, right maxilla*). — The simple and lobular exopodite has six widely spaced plumose setae. The unsegmented endopodite has four sparsely plumose terminal setae and two subterminal setae. There are two endites. The basal endite (distal) has four and five setae on its distal and proximal lobes respectively. The coxal endite (proximal) has four and eight setae on its distal and proximal lobes respectively. The maxillule and maxilla are described and illustrated only for stage I zoeae.

First maxilliped (*Fig. 1g*). — The exopodite has four long, heavily plumose setae. Setae on the exopodites of the maxillipeds, when present, are always terminal. The endopodite is five-segmented and equal in length to the exopodite. The setation formula of the endopodite is 6, 2, 2, 5, 2. The basis has nine small setae on its ventral surface.

Second maxilliped (*Fig. 1h*). — The exopodite has four long, heavily plumose setae. The four-segmented endopodite is slightly shorter than the exopodite. The setation formula of the endopodite is 5, 2, 2, 2. The basis has three setae ventrally on the distal half of the segment.

Third maxilliped (*Fig. 1h*). — The third maxilliped is composed of two segments, the basis and the exopodite, and has no setae. The endopodite is evident only as a slight extension of the basis and is not segmented from the basis.

Pereiopods (*Fig. 1a*). — The developing pereiopods are present beneath the carapace, and the tip of the first pereiopod is already bifid. None of the pereiopods are segmented at this stage.

Abdomen and telson (*Fig. 1i*). — Segments 2–5 have one pair of lateral and two pairs of dorsal spines on their posterior margins. Some variation exists in the dorsal spination of the abdomen. For example, an "extra," unpaired spine is sometimes present. The lateral spines are progressively longer on the more posterior segments. Those of the fifth segment extend posteriorly to the level of the anus. The posterior margin of the telson is cleft medially to form the slight lateral lobes characteristic of many lithodid larvae. Terminally, each of the paired lobes has nine telson processes. The first (lateral) process, a spine, is not articulated; the second is small and hair-like. This second process was first recorded in zoeae of *P. platypus* by Kurata (1964). The medial seven telson processes on each lobe are articulated spines with small denticulations basally. The fourth process (the third spine) from the lateral margin of each telson lobe is at least one-third longer than any of the other telson processes.

Pleopods and uropods are not evident on stage I zoeae.

The number of segments and their spination, as well as the number and distribution of the telson processes are the same in all zoeal stages. Because the changes are few and the descriptions long, the telson processes are not described for each stage.

STAGE II ZOEA

At this stage (Fig. 2*a*) the average carapace length is 1.3 mm (33 specimens); the average total carapace length is 3.4 mm (9 specimens); and the average total body length is 5.2 mm (10 specimens). The eyes are stalked and movable in this and all subsequent stages.

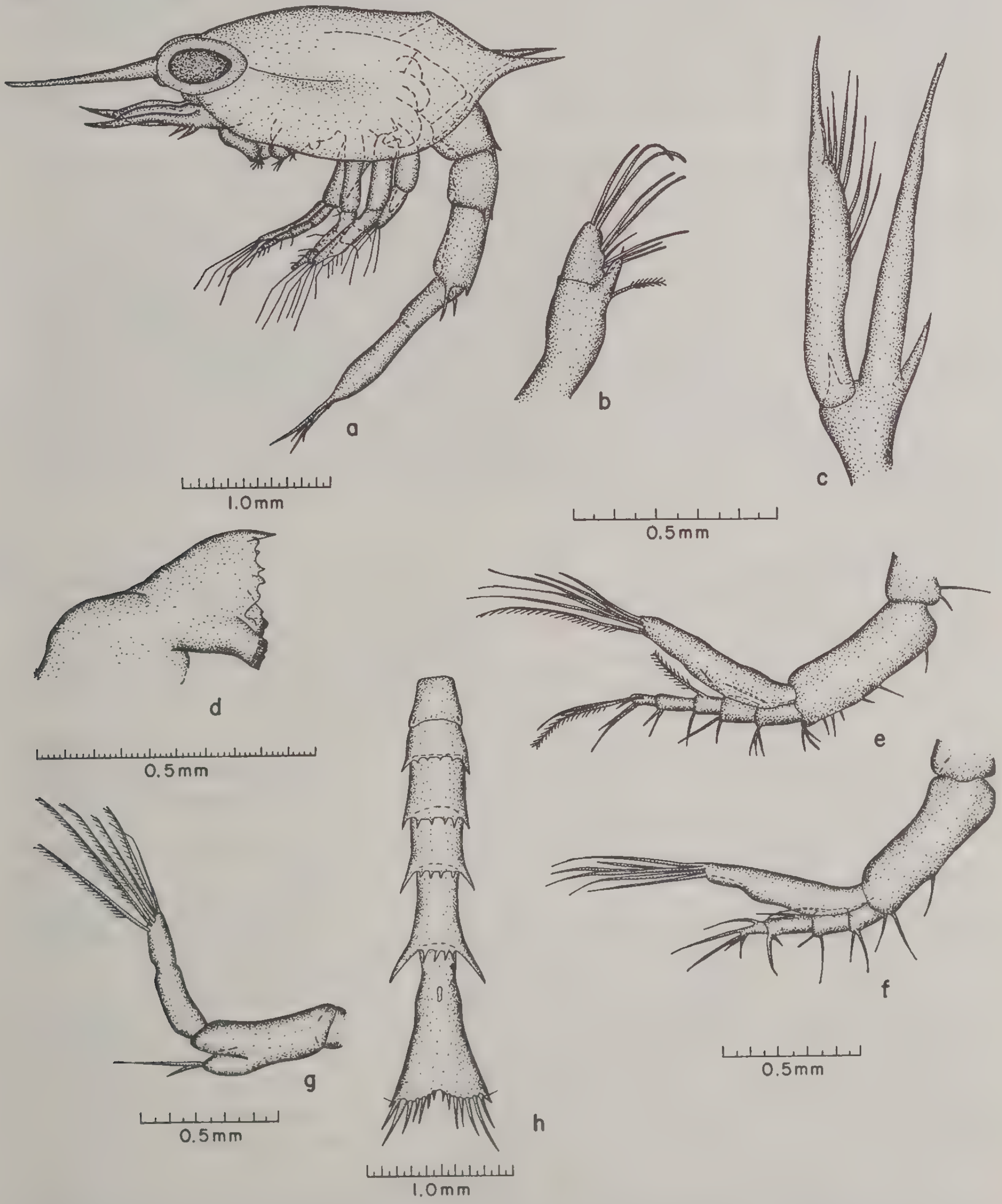

FIG. 2. (*a*) Stage II zoea of *P. platypus*; (*b*) antennule; (*c*) antenna; (*d*) mandible; (*e*) first maxilliped; (*f*) second maxilliped; (*g*) third maxilliped; (*h*) abdomen and telson.

Antennule (*Fig. 2b*). — The outer distal segment of the antennule has eight aesthetes and at least two setae. Terminal setae are lacking on the lobe of the proximal segment, although in some individuals a single sparsely seta lies at the base of this lobe. The lobe is slightly longer than one-half the length of the distal segments.

Antenna (*Fig. 2c*). — The antenna is similar to that of stage I zoeae. The basal segment has two stout spines. Only the medial one is segmented from the basis, and this spine has small spinules on its distal half. The lateral spine is the smaller and is smooth. The exopodite has eight sparsely plumose setae on the medial margin and terminates in a long, slender projection which extends beyond the end of the endopodite. The narrow endopodite is not segmented from the basis, and the tip of the endopodite is slightly bifid. The exopodite and endopodite are of subequal length.

Mandible (*Fig. 2d*). — The antero-dorsal portion of the mandible has several teeth dorsally. The molar process, which had large teeth in stage I, now consists of three sections, each with numerous tubercles.

First maxilliped (*Fig. 2e*). — The exopodite has six long, heavily plumose terminal setae. The endopodite is five-segmented and equal in length to the exopodite. The setation formula of the endopodite is 5, 2, 2, 3, 4. The basis has nine small setae on its ventral surface.

Second maxilliped (*Fig. 2f*). — The exopodite has six long, heavily plumose setae. The endopodite is four-segmented and slightly shorter than the exopodite. The setation formula of the endopodite is 5, 3, 3, 2. The basis has three setae ventrally on the distal half of the segment.

Third maxilliped (*Fig. 2g*). — The exopodite has six plumose terminal setae. The endopodite arises from the side of the basis and does not extend beyond the basis. Terminally, the endopodite has one long and one short seta. The endopodite is not segmented from the basis.

Pereiopods (*Fig. 2a*). — The pereiopods are larger than in stage I but have the same form. The tip of the first pereiopod is bifid.

Abdomen and telson (*Fig. 2h*). — The abdomen and telson are similar to those of stage I. Tissue buds of the developing pleopods and uropods can be seen within the exoskeleton.

STAGE III ZOEA

Stage III zoeae (Fig. 3*a*) have an average carapace length of 1.6 mm (10 specimens); an average total carapace length of 3.5 mm (5 specimens); and an average total body length of 5.5 mm (5 specimens).

Antennule (*Fig. 3b*). — The distal segment of the antennule has eight aesthetes and two or three setae. The medial extension or lobe of the proximal segment is about two-thirds the length of the distal segment and has a single plumose seta at its base.

Antenna (*Fig. 3c*). — The shape, spination, and setation of the antenna resemble those of stages I and II. The basal segment has two stout spines. Only the medial one is segmented from the basis, and this spine has small spinules on its distal half. The smaller lateral spine is smooth. The exopodite and endopodite are subequal in length.

Mandible (*Fig. 3d*). — The mandible is similar to that of stage II. It has a well-developed molar process. There is no indication of a developing mandibular palp.

First maxilliped (*Fig. 3e*). — The exopodite has six long, heavily plumose terminal setae. The endopodite is five-segmented and equal in length to the exopodite. The setation formula of the endopodite is 5, 2, 2, 3, 4. The basis has nine small setae on its ventral surface.

Second maxilliped (*Fig. 3f*). — The exopodite has six long, heavily plumose setae. The endopodite is four-segmented and slightly shorter than the exopodite. The setation formula of the endopodite is 5, 3, 3, 2. The basis has three setae ventrally on the distal half of the segment.

Third maxilliped (*Fig. 3g*). — The exopodite has six plumose terminal setae. The endopodite arises from the midpoint of the side of the basis and extends beyond the end of the basis. The endopodite is not segmented from the basis; terminally it has one long and one short seta.

Pereiopods (*Fig. 3h*). — The pereiopods are larger relative to the rest of the body than in the previous stages, but segmentation is not visible. The cheliped is now the most prominent of these appendages, and the dactylus and its propodal extension, the opposed spine, are apparent.

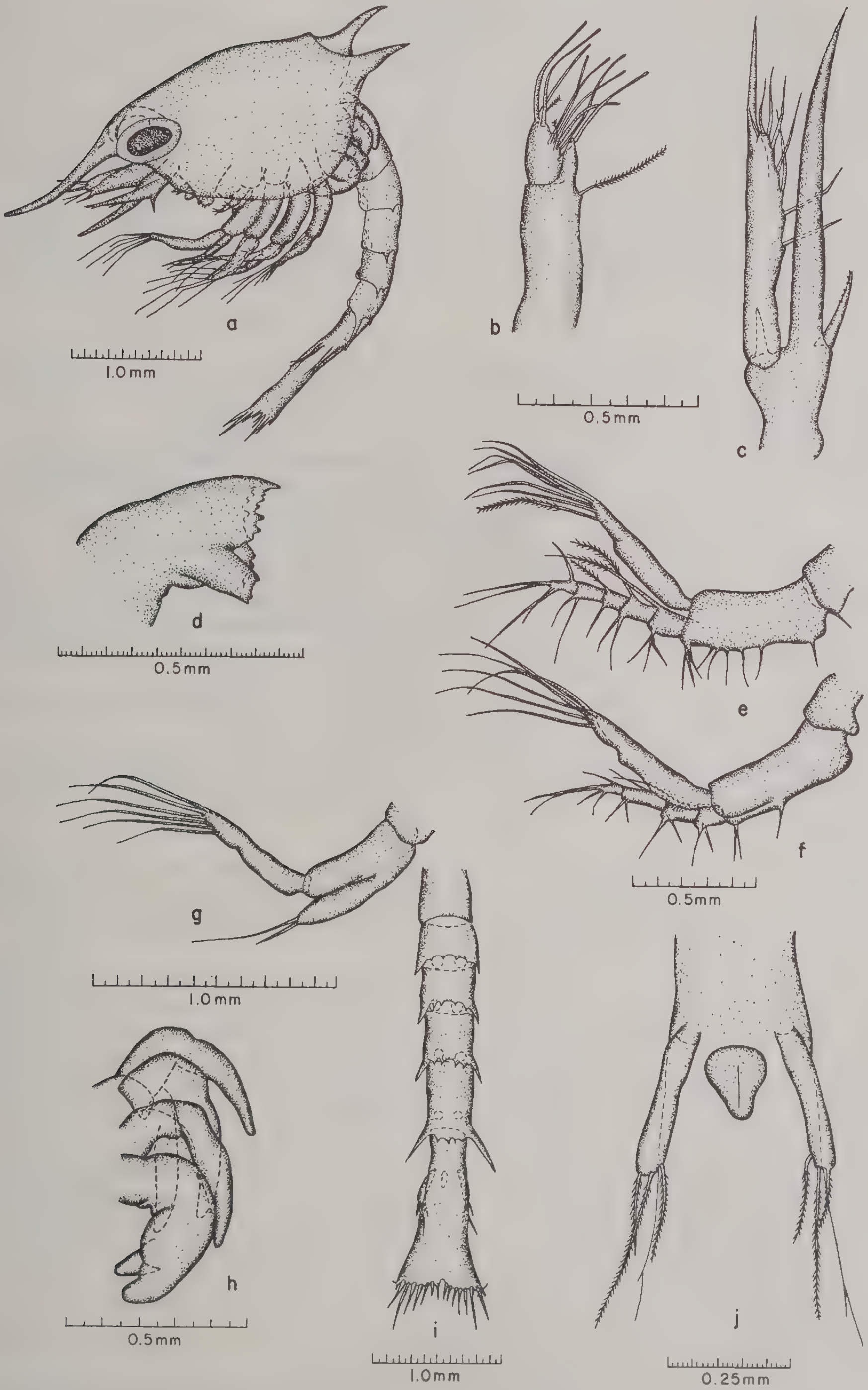
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FIG. 3. (*a*) Stage III zoea of *P. platypus*; (*b*) antennule; (*c*) antenna; (*d*) mandible; (*e*) first maxilliped; (*f*) second maxilliped; (*g*) third maxilliped; (*h*) pereiopods; (*i*) abdomen and telson; (*j*) uropods.

Abdomen and telson (Fig. 3i). — The abdomen and telson are similar to those of stages I and II except for the addition of the pleopod buds and the uropods. The pleopod buds are on the postero-ventral region of abdominal segments 2 through 5. The uropods are on the telson lateral to the anterior lip of the anus.

Pleopod buds (Fig. 3a and 3i). — Pleopod buds generally show as small bumps on the exoskeleton of the abdomen and as internal tissue buds; the bumps are present in the stage III exuviae. In a few specimens, which may be abnormal, the pleopods appear only as tissue buds beneath the exoskeleton and are not evident on the exoskeleton.

Uropods (Fig. 3i and 3j). — The uropods, first present in stage III, are each composed of a single segment. Each bears three plumose setae, two terminal and one subterminal. The middle seta on each uropod is approximately twice as long as the lateral and slightly less than twice as long as the medial seta.

STAGE IV ZOEA

The average carapace length of stage IV zoeae (Fig. 4*a*) is 2.0 mm (8 specimens); the average total carapace length is 4.5 mm (8 specimens); and the average total body length is 6.8 mm (8 specimens).

Antennule (Fig. 4b). — The distal segment of the antennule has eight or nine aesthetes and two setae. The medial extension or lobe of the proximal segment and the distal segment are subequal in length. The medial extension has a plumose seta at its base.

Antenna (Fig. 4c). — The antenna is similar in shape, setation, and spination to that of previous stages. The basal segment bears two stout spines. The medial spine is segmented from the basis, and the distal half is denticulate. The lateral spine is smaller, smooth, and not segmented from the basal segment. The exopodite has eight sparsely plumose setae on the medial margin and terminates in a long, slender spine which makes the exopodite and endopodite subequal in length.

Mandible (Fig. 4d). — The mandible is similar to that of the previous two zoeal stages. The molar process is well developed. A mandibular palp is not present.

First maxilliped (Fig. 4e). — The exopodite has six long, heavily plumose terminal setae. The endopodite is five-segmented and equal in length to the exopodite. The setation formula of the endopodite is 5, 2, 2, 3, 4, as in zoeal stages II and III. The basis has nine small setae on its ventral surface.

Second maxilliped (Fig. 4f). — The second maxilliped is the same as in stages II and III. The exopodite has six long, heavily plumose setae. The endopodite is four-segmented and shorter than the exopodite. The setation formula of the endopodite is 5, 3, 3, 2. The basis has three setae located on the distal half of its ventral margin.

Third maxilliped (Fig. 4g). — The exopodite has six plumose terminal setae. Some indication appears of segmentation of the endopodite from the basis, but segmentation is not yet complete. The endopodite has three sparsely plumose setae, two terminal and one subterminal.

Pereiopods (Fig. 4a). — The relative size of the pereiopods has increased so that they now project below the margin of the carapace. The pereiopods have all segments of the adult stage. None of the pereiopods have setae. The cheliped, pereiopod 1, has two rows of denticles on the inner surface of the dactylus and its propodal extension. Within each of the pereiopods 2 to 5, all segments are about the same diameter except the terminal segment, which is always smaller.

Abdomen and telson (Fig. 4h). — The abdomen and telson of stage IV zoeae have spination and setation similar to those of earlier stages. Abdominal segments 2 through 5 bear pleopods. The uropods are on the telson just anterior and lateral to the anus. The anterior portion of the telson of the zoea is destined to be the sixth abdominal segment of the glaucothoe.

Pleopods (Fig. 4h and 4j). — The pleopods are composed of two segments and bear no setae. Each pleopod has an extension on the medial side of the proximal segment. This extension becomes the endopodite of the pleopod in the glaucothoeal stage.

Uropods (Fig. 4h and 4i). — The uropods are two-segmented: the proximal segment is slightly less than one-half the length of the distal segment. The distal segment of each uropod has three plumose setae. Both the lateral and the medial setae are about two-thirds the length of the median seta.

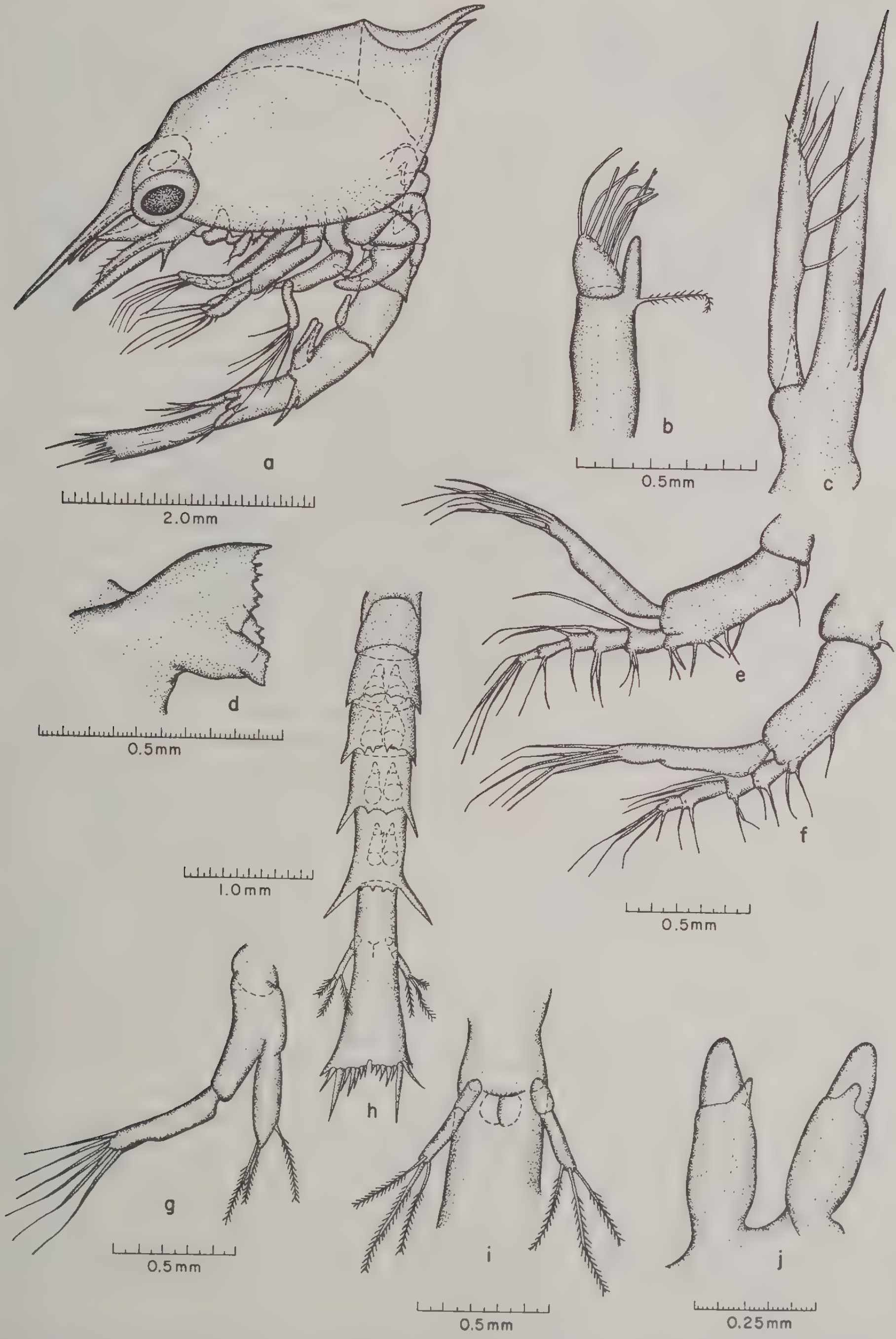
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FIG. 4. (*a*) Stage IV zoea of *P. platypus*; (*b*) antennule; (*c*) antenna; (*d*) mandible; (*e*) first maxilliped; (*f*) second maxilliped; (*g*) third maxilliped; (*h*) abdomen and telson; (*i*) uropods; (*j*) pleopods of fifth abdominal segment.

GLAUCOTHOE

The glaucothoes (Fig. 5 and 6) have an average carapace length of 1.8 mm (6 specimens), 0.2 mm less than the comparable measurement of stage IV zoeae. A decrease length with the change in body form from zoea to glaucothoe is usual in larvae of *Paralithodes*. The average total carapace length is 2.6 mm (six specimens). The average width of the carapace of the glaucothoes is 1.7 mm (six specimens). The total lengths of the glaucothoes were not determined because death causes the abdomen to be flexed so tightly against the ventral surface of the body that accurate measurements cannot be made.

The carapace (Fig. 5*a* and 6*a*) of the glaucothoe has 15 pairs of spines on its dorsal surface, not including those of the rostral complex (frontal area of Makarov, 1938). This complex is discussed separately. In addition to the dorsal spines, the antero-ventral margin of the carapace has a pair of suborbital spines. Each of the spines on the carapace has a small seta on its base. The number of paired spines on the carapace of the glaucothoe was constant on all specimens examined, although their location was slightly variable. The carapace spination is described according to the carapace areas in crab-like anomurans designated by Makarov (1938). The 15 pairs of dorsal spines are disposed as follows: two pairs in the gastric area and two pairs in the cardiac area disposed in two parallel lines from anterior to posterior; one pair in the orbital area; two pairs in the hepatic area; and eight pairs in the branchial areas. Four of the pairs of spines in the hepatic and branchial areas are on the lateral margins of the carapace; the most anterior pair is in the hepatic areas. and the other three pairs are in the branchial areas.

The rostral complex of the carapace (Fig. 6*b* and 6*c*) includes two antero-lateral prominences or, spines, each of which has a smaller, medio-dorsally directed spine. Each of these four spines has a small seta on its base. The rostral spine is well developed and is about equal in length to the truncate base of the complex from which it originates. The eyes each have four spines on their anterior surface, and each of these spines has a small seta.

Antennule (Fig. 5b). — The antennule of the glaucothoe is composed of a three-segmented peduncle which terminally has a pair of segmented rami. The larger ramus is four-segmented. The distal segment has three terminal setae and three lateral aesthetes, and the next two more proximal segments have at least six aesthetes each. The basal segment of the larger ramus has neither setae nor aesthetes. The smaller ramus of the antennule is two-segmented. The distal segment has three large terminal setae and six small setae, and the proximal segment has two setae. The peduncle has two small setae (neither of which is plumose), one on each of its two most distal segments. The outermost seta of the peduncle is in the position of the large plumose seta of the antennular peduncle of the zoea.

Antenna (Fig. 5c). — The antenna of the glaucothoe differs considerably from that of the zoea. The endopodite is now an elongate, nine-segmented flagellum rather than unsegmented as in the zoea. This flagellum has setae on all segments except the third from the basis. The exopodite (antennal scale) is smaller than in the zoea and has one simple seta. The prominent spines that were on the basis in earlier zoeal stages are also smaller, particularly the one below the flagellum.

Mandible (Fig. 5d). — The mandible of the glaucothoe has a well-developed, two-segmented mandibular palp which has no setae. This stage is the first in which the mandibular palp is present. The denticles on the mandible are relatively smaller than those of the zoeal stage.

First maxilliped (Fig. 5e). — The first maxilliped is smaller than it is in the zoeae. The two-segmented exopodite has five short plumose setae. The two-segment endopodite has four short terminal setae. The exopodite and endopodite both appear shriveled, and their segmentation is difficult to determine because of folds in the exoskeleton. The basis has six small setae.

Second maxilliped (Fig. 5f). — The second maxilliped is relatively smaller in the glaucothoeal stage than in the zoeal stages. The exopodite is two-segmented and has five sparsely plumose terminal setae. The endopodite is four-segmented and has one short terminal seta. The basis has no setae.

Third maxilliped (Fig. 5g). — The third maxilliped as a whole is relatively larger than in the zoeal stages; but the two-segmented exopodite, which has five terminal setae, is relatively smaller. The endopodite is larger and more highly developed than in previous stages and is seg-

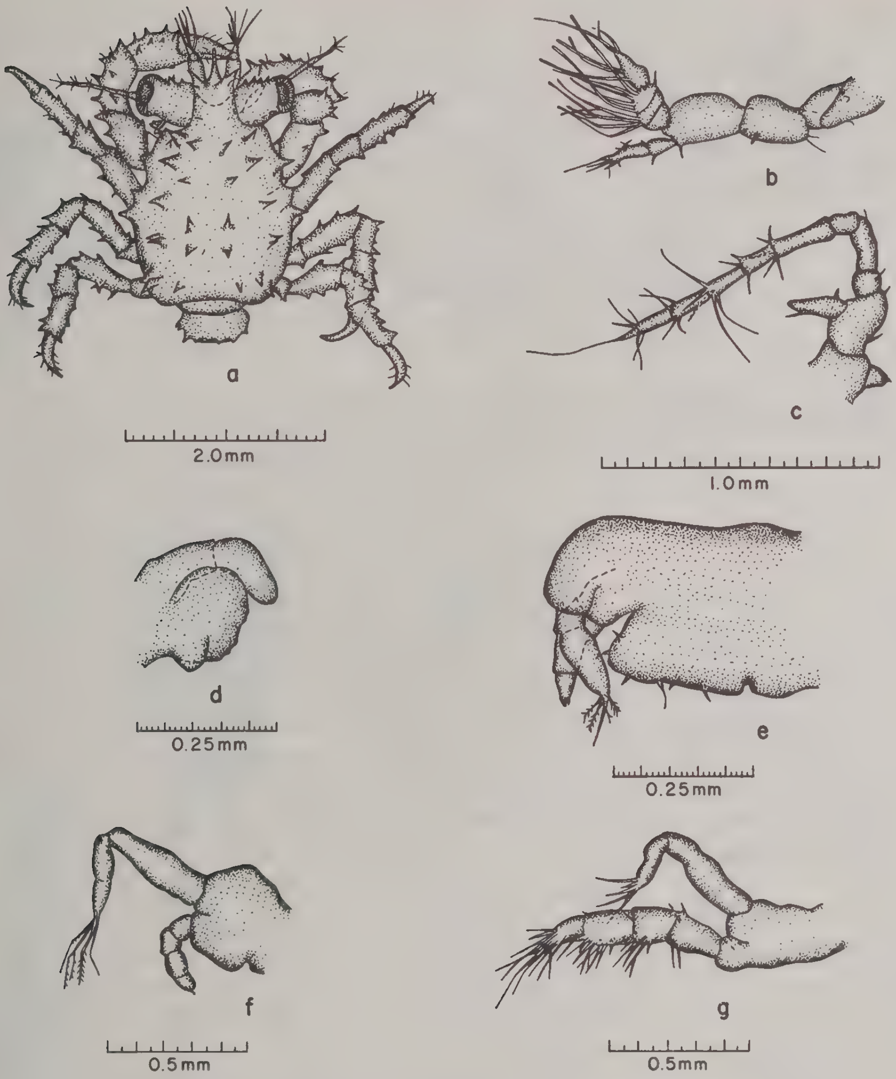

FIG. 5. (*a*) Glaucothoe of *P. platypus*; (*b*) antennule; (*c*) antenna; (*d*) mandible (right); (*e*) first maxilliped; (*f*) second maxilliped; (*g*) third maxilliped.

mented for the first time. The endopodite is composed of four segments, each with robust denticulate setae. The setation formula of the endopodite is 10–14, 10–14, 7, 4, and the setae are concentrated on the ventral surface.

Pereiopods. — The pereiopods closely resemble those of the adult. Pereiopods 1–4 (Fig. 5*a*) bear spines on all segments except the dactyls. The dactyls of pereiopods 1–4 are setose. The right cheliped is larger than the left, but has a similar form. The fifth pereiopod (Fig. 6*d*) is held beneath the carapace in this stage as in post-larval stages. The fifth pereiopod is six-segmented and has setae on the distal three segments; it also has two short simple setae on each dactyl, three long terminally curved setae and six shorter setae on each propodus, and a single seta on each carpus.

Abdomen and telson (Fig. 6e). — The segmentation of the abdomen and the spination of the abdomen and telson differ those of zoeal stages. The abdomen is now six-segmented, and

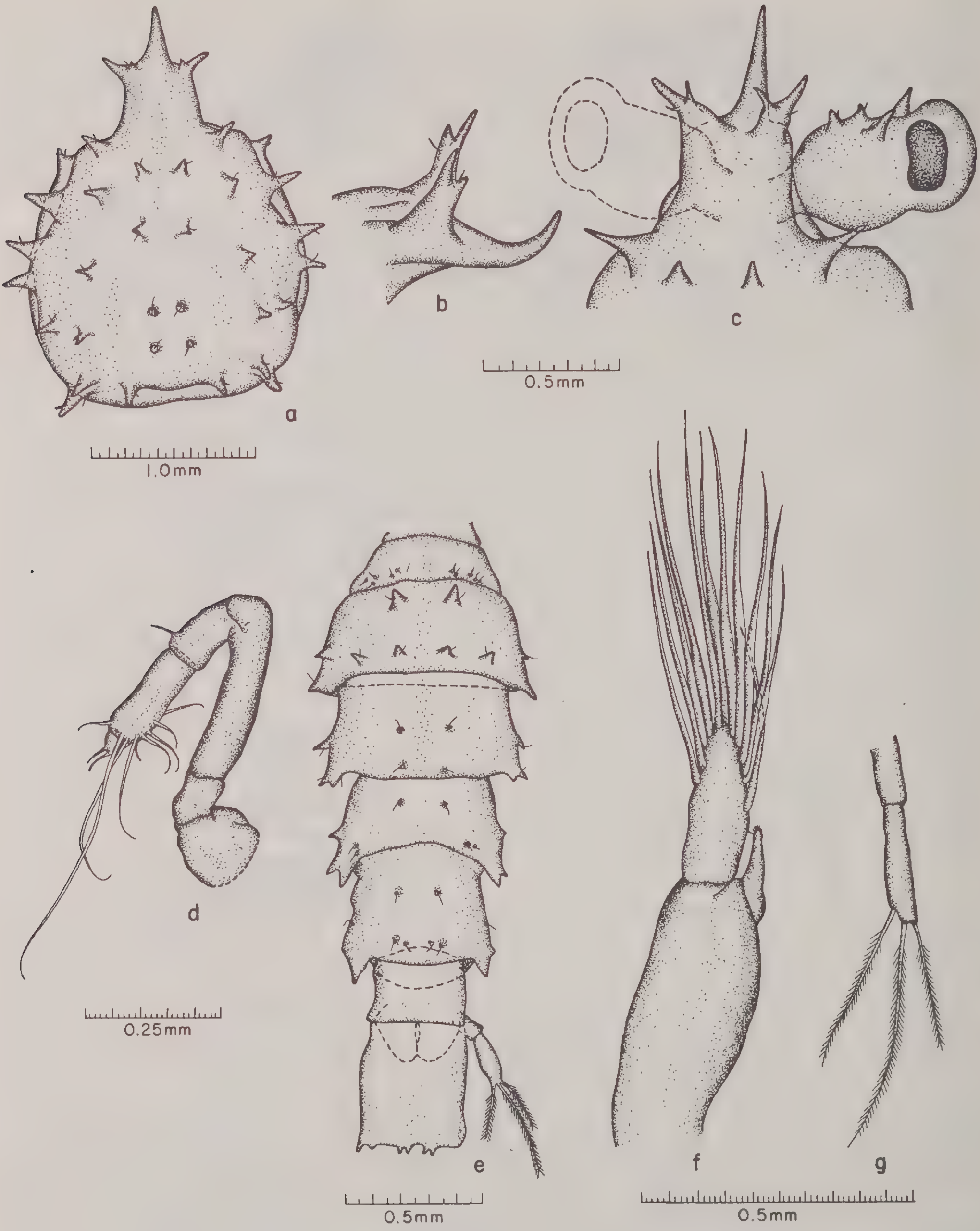

FIG. 6. (*a*) Carapace of glaucothoe of *P. platypus*; (*b*) rostrum; (*c*) eye and rostrum complex; (*d*) fifth pereiopod; (*e*) abdomen and telson; (*f*) pleopod; (*g*) uropod.

the uropods arise from the sixth segment. All abdominal segments have hair-like setae on the dorsal surface. On the second segment these setae occur at the bases of the three pairs of dorsal spines. The spines on this segment are located as follows: one on each side of the midline in the antero-dorsal region and two on each side of the midline in the postero-dorsal region. Each lateral margin of the second segment has two spines, one somewhat posterior to the middle of the segment and the other on the postero-lateral corner. The postero-lateral corners of segments 3, 4, and 5 are prolonged into backward pointing spines which are bifid in segments 3 and 4. The postero-lateral corners of segments 1 and 6 do not have spines. The setation of the telson varies, but setae are fewer and smaller than in the zoea. The posterior margin of the telson has as few as two pairs or as many as five pairs of setae. A consistent feature of the telson in all larval stages is a seta-free median notch in the posterior margin. This notch is broader and shallower in the glaucothoe than in the zoea.

Pleopods (*Fig. 6f*). — Pleopods are present on abdominal segments 2 through 5, as in zoeal stages III and IV, but are more highly developed. The exopodites of the pleopods 2 through 5, respectively, have 12, 12, 13, and 11 large plumose terminal setae which are not present on the zoeal pleopods. The endopodite, now segmented from the proximal segment of each pleopod, consists of a single segment with three short, stout, hooked setae and one simple seta on the distal end.

Uropods (*Fig. 6e and 6g*). — The uropods are similar to those of stage IV zoea. They are two-segmented; the distal segment of each has three long plumose setae. The lateral seta is slightly more than two-thirds, and the distal seta slightly less than two-thirds, as long as the medial seta.

COMPARISON OF DESCRIPTIONS OF LARVAE OF *P. PLATYPUS*

Rearing the larvae of *P. platypus* in the laboratory permitted the verification or correction of some earlier descriptions of the zoea. My materials also provided a basis for more description of the development of the zoea and the first description of the glaucothoe. The development of the larvae of *P. platypus* is similar to that of other species of the family Lithodidae. Gurney (1942), Pike and Williamson (1959), MacDonald et al. (1957), and Hart (1965) discussed similarities of larval development among the species of Lithodidae. My discussion is limited therefore to the differences among the various descriptions of the larval development of *P. platypus* and some similarities within the genus *Paralithodes*.

The larvae described in this study differ in several ways from the descriptions of Marukawa, Sato, and Kurata. The differences may arise partly from the sources of the specimens described. Marukawa (1933) used stage I zoea whose origin is unknown to me. The first zoeae used by Kurata (1964) were from the plankton. Sato (1958) obtained zoeae of stages II–IV from the intestinal tracts of juvenile pink salmon.

Marukawa (1933) presented a figure of the whole stage I zoeae of *P. platypus* but illustrated in detail only the telson and antenna. The arrangement of telson processes that I found are like those shown in Marukawa's figure except that his figure lacked the 2nd hair-like telson process. Marukawa did not describe the appendages of *P. platypus* in his text. The antenna was illustrated by Marukawa with two well-developed spines on its basal segment, but the proximal one lacked the denticulations that I found. Points of agreement between Marukawa's description and mine are the eight setae on the medial margin of the antennal scale and the subequal lengths of the exopodite (antennal scale) and the endopodite. The tip of the endopodite in Marukawa's figure is simple, rather than bifid as I have found. This difference may be a matter of individual variation rather than a specific character. The average total body length of stage I zoeae in the present study (4.88 mm) is similar to that found by Marukawa (4.98 mm). Carapace lengths cannot be compared because the points from which Marukawa's measurents were made are not stated.

Kurata (1964) described only the stage I zoea of *P. platypus*. He indicated that this stage had 9 + 9 telson processes. I found these numbers to apply in all the zoeal stages. The lateral spines of the fifth abdominal segment of my stage I zoeae were longer than those described by Kurata. He stated that they reach approximately three-fourths of the distance to the anterior lip of the anus, but I found that although these spines were variable, they generally extended to the level of the anterior lip of the anus (all zoeal stages). Kurata found nine setae on the medial margin of the antennal scale, whereas I found eight.

Sato (1958) did not describe in detail the zoeal stages of his specimens (from the intestinal tracts of juvenile pink salmon); only his illustrations are available, therefore, for comparison with my larvae.

The most striking difference between Sato's (1958) zoeal material and mine is the larger size of the lateral spines of abdominal segments 3 and 4 in my specimens. The lateral spination of the abdominal segments of *P. platypus* illustrated by Sato resembles that of *P. camtschatica* more than that of my specimens. The sixth abdominal segment is separated from the telson in zoeal stages III and IV in Sato's figures, but I did not find this separation until the glaucothoeal stage.

I found the following differences between the setation of Sato's (1958) figures and mine: Sato showed nine setae on the antennal scale instead of the eight I consistently found in all zoeae. Sato illustrated the exopodites of maxillipeds 1–3 in stage II zoeae with 7, 7, and 6 setae and all maxillipeds of stages III and IV with eight plumose setae on each of the exopodites. In contrast, I found 4, 4, and 0 plumose setae on exopodites of maxillipeds 1, 2, and 3, respectively, in zoeae of stage I, and six plumose setae on the exopodite of maxillipeds 1, 2, and 3 in all other zoeal stages. The uropods of the stage III zoeae illustrated by Sato have three short spines rather than the three long slender plumose setae I found.

One of the few morphological features present in all of the developmental stages of the three species of *Paralithodes* whose larval development has been studied is the medial notch of the posterior margin of the telson. This notch was once thought to be characteristic of all species of the family Lithodidae, but larvae of *Cryptolithodes typicus* do not have it (Hart, 1965).

In the genus *Paralithodes*, some species have three and others four zoeal stages. The uropods of these zoeae are always uniramous and have three setae. The uropods of the last zoeal stage always have two segments. They have one segment in stage III in those species with four zoeal stages. Species with three zoeal stages lack uropods in stage II.

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Jefferson J. Gonor and Josephine F. L. Hart reviewed the manuscript and offered many helpful suggestions; Jiro Nishimoto and George Kudo translated portions of the Japanese works cited; and Elmer L. Landingham prepared the illustrations from my original camera lucida drawings.

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Annulus Formation on Scales of Four Species of Coregonids Reared Under Artificial Conditions[1,2]

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ABSTRACT

Scales from known-age coregonids reared in the laboratory were examined to determine when annuli formed and to learn possible factors of their formation. Scales were taken monthly from marked fish for periods up to 21 months. Scales were also examined from fish that died and from preserved specimens of young-of-the-year for each species. Two marks formed on almost all scales each calender year. The stronger formed during March–April and the weaker in October–November. Both marks had all the usual characteristics of an annulus but the spring mark was considered the annulus and the fall mark an accessory check. The annulus formed during a period of constant temperatures and of little change in growth or increasing growth. The accessory check formed during a period of declining temperatures (1–5 degrees F, or 0.6–2.8 degrees C, per month) and of little change in growth or declining growth. Most fish grew throughout the winter; the only exceptions were one bloater (*Coregonus hoyi*) and several of the largest lake whitefish (*C. clupeaformis*). Fish were always given all the food they would eat to eliminate availability of food as a factor of mark formation. The temperature of the water during the winter (50 ± 0.3 F; 10.0 ± 0.2 C) did not arrest metabolic activity. The growth rate was related more closely to day length than to other variables examined.

INTRODUCTION

This study is based on scales from known-age coregonids (lake whitefish and ciscoes) reared at the U.S. Bureau of Commercial Fisheries Biological Station at Northville, Michigan. The study was initiated to determine if the fish formed annuli, and to find possible relationships between annulus formation and environmental conditions.

Van Oosten (1923) established the time of annulus formation for lake whitefish (*Coregonus clupeaformis*) reared in aquariums and later (1929) made a critical evaluation of the scale method for age determination of the lake herring (*C. artedi*) of Lake Huron. The basic assumptions inherent in the scale method and the views on factors of annulus formation developed by Van Oosten are mostly held valid today. The present study indicated, however, that length of day, not previously thought to influence annulus formation, may be an important factor for the coregonids.

Life histories have been studied for at least one population of most species of coregonids of the Great Lakes, but few of the studies established the time

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of annulus formation and none included experimental data on the formation of the marks used to estimate age and calculate growth. Evidence is provided here which emphasizes the need for careful validation of the year-mark on some populations of wild coregonids.

MATERIALS AND METHODS

The three species and one hybrid investigated were lake whitefish, bloater, kiyi (*C. kiyi*), and the first generation of a cross between female lake herring and male bloater.

In June or early July 1962, the largest fish in each of nine tanks, each containing various year-classes and species, was anesthetized, inoculated with antibiotics, measured, and injected with experimental orange dye (composition unknown to me). In September 1962, three young-of-the-year whitefish were similarly marked. Each month (with few exceptions) one or two scales were taken from the left side of each marked fish, between the dorsal fin and lateral line. If a marked fish died, the next largest fish in that tank was marked and a new series was started.

Scales were taken from 16 marked fish, including at least two individuals of each species and the hybrid (Table I). The number of scale samples from individual fish ranged from 3 to 17 over periods up to 21 months. A total of 137 scale samples from the marked fish was examined.

Scale samples were also obtained from unmarked fish that shared the tanks with the marked ones. When a fish died it was measured, labeled, and preserved. Scales for study were removed from two or three fish of each species that died each month through 1963. Scales from young-of-the-year of each species were also examined to determine scale development before the first annulus. A total of 288 scale samples from unmarked fish was used.

A correction factor of 1.023 was used to adjust the lengths of preserved fish before the regression equations of the body-scale relation used for back calculation of lengths were computed. This factor was determined by measuring 38 lake whitefish (250–400 mm long), 105 bloaters (100–250 mm), and 49 hybrids (100–300 mm) on the date of death and after preservation in 10% formalin for 1–3 years, when shrinkage had stabalized (Parker, 1963). Marked fish were measured alive at time of scale removal.

Cellulose acetate impressions were made of all scales (Smith, 1954) and examined at a magnification of 41× on a microprojector (Moffett, 1952). Two to five scales were examined from each unmarked fish and one or two scales for each date of removal from the marked fish. Application of several drops of acetone to the plastic strip, before impressing the scales, increased the clarity of the magnified image. Designation of age-groups followed the conventional practice which assumes that a fish becomes 1 year older on January 1 (Hile, 1936).

All fish were always fed as much as they would eat and all ate throughout the year.

TABLE I. Numbers of scale samples taken from various species of marked coregonids and periods of collection.

Species and year-class	Specimen no.	Period of collection	No. of months lived after marking[a]	No. of scale samples taken
Lake whitefish				
1962	1	9/14/62–5/1/63	8	4
1962	2	9/17/62–1/27/64	17	12
1962	3	9/17/62–12/10/63	16	9
1962	4	7/3/63–1/24/64	7	7
1959	5	6/8/62–12/10/63	19	17
1958	6	6/8/62–1/25/63	8	7
1958	7	6/8/62–2/28/64	21	16
Bloater				
1961	8	6/11/62–4/8/63	11	10
1961	9	7/5/63–3/7/64	9	8
1960	10	7/9/62–5/28/63	11	12
Lake herring × bloater hybrid				
1961	11	6/11/62–9/14/62	4	3
1961	12	6/13/62–1/15/63	8	7
1961	13	10/15/62–7/5/63	10	8
1961	14	8/9/63–2/6/64	7	6
Kiyi				
1961	15	6/8/62–4/8/63	11	8
1961	16	7/10/62–9/17/63	15	13
Total				137

[a] Includes months of marking and death.

The temperature of the spring water at the Northville station was 50 F (10 C). The water was sprayed into a large cement raceway and then pumped to the rearing troughs and tanks, or was taken by gravity feed from a large holding pond. Daily water temperatures for each tank were averaged by 10-day intervals.

A detailed account of methods, data, and analyses is given in the thesis upon which this paper is based (Hogman, MS, 1965).

TIME OF ANNULUS FORMATION

Almost all the scales had two strong marks each year, more than could be accounted for as annuli. The diameter increments within the two most recent marks and the total anterior-posterior diameter on each scale were measured along an imaginary line that passed through the focus and bisected the anterior and posterior fields (Van Oosten, 1929). After the scales of all groups of fish had been examined twice (randomly for each species) the percentage increase in scale diameter beyond the last mark was calculated for scales collected each month. The percentage increases for each fish were then arranged chronologically. Check formation was indicated when the percentage increase beyond the outermost mark dropped suddenly and then began to increase again.

A check that represented the true annulus (Fig. 1A, B) began to form on all species in late March 1963, and had usually circled the scale by mid-April. The earliest indication of annulus formation was on March 12, 1963, for a age-I whitefish. Annulus formation was not complete for some fish longer than 250 mm until late April. Fish entering their second through fourth growing seasons (age I–III) formed annuli slightly earlier than seven marked specimens age IV and older examined at or just after annulus formation.

All unmarked fish over 1 year old had the same pattern of dual marks on their scales for all years of life. The percentage increases in scale diameter beyond the outer mark could not be averaged for the unmarked fish because of the small number (1–3) available (that had died) each month for each species; and because of the great differences in growth of individual fish. However, direct observation of scales from unmarked fish collected before and after annulus and accessory check formation of the marked fish, indicated that they also formed their annulus in late March – early April and an accessory check in late October – early November.

Scales from fish that had ceased growing or were growing very slowly preceding annulus formation (three large whitefish and two bloaters) suggested that scale growth resumed before a measurable increase was detectable in the total length. The data did not permit evaluation of the relation of size within an age-group to time of annulus formation.

To determine the validity of annulus identification and provide further evidence for time of occurrence, the lengths of the marked fish were back-calculated for the 1962 and 1963 annuli and compared with known lengths at various dates. This method indicated that the 1962 annulus formed in March or April. The identification of the 1963 annulus, for all scales collected after April, was confirmed in like manner. Although fish were not marked until June 1962, they were measured monthly beginning in March 1962. By comparing the average back-calculated length (at the 1962 annulus) with the size of the largest fish in the tank for the months before June 1962, the March–April formation of the 1962 annulus was confirmed. The marked fish always maintained their size advantage over others in the tank after June 1962; therefore the assumption that they were also the largest during March to June seems warranted. A retention of size advantage has been demonstrated for brown trout (*Salmo trutta*) reared under artificial conditions (Brown, 1946).

The number of annuli on each fish corresponded to its age. Many fish exhibited highly distinct annuli (Fig. 1A and 3A), but most scales were more difficult to interpret. Often the year-mark was so faint it might have been overlooked on wild fish of unknown age.

TIME OF ACCESSORY CHECK FORMATION

An accessory check (Fig. 1, 3) was formed in the fall on scales of nearly all fish studied. Formation of the mark began in mid-October and was complete by mid-November.

The mark was absent (Fig. 2) on scales of three young-of-the-year whitefish in September 1962 but an accessory check had formed by early November. The first annulus formed in late March 1963. Scales from two of these fish that lived through the following fall showed only two strong marks (check and annulus) on September 5 (Fig. 3A) and October 7, but scales taken on November 4 had an additional strong check inside the margin (Fig. 3B).

The accessory check was not as well defined as the annulus but it could nearly always be detected. Comparison of calculated lengths from accessory checks with actual measurements in various months, verified the period when the checks were formed. Scales from unmarked fish that had died mid-November to January (all species and years) also had an accessory check just inside the margin. The widely spaced ridges between A2 and the next outer accessory check (*ac*) on Fig. 1 are commonly found in coregonid scales and reflect periods of fast growth (Van Oosten, 1923, 1929; Moffett, 1952). Seventeen sets of scales were taken from this fish (specimen 5, Table I) and they all showed the same characteristics and reflected very rapid growth during the early summer of 1961 at age II.

Accessory checks were not reported by Van Oosten (1923) on whitefish reared in the New York Aquarium, but they are known to occur for many lake populations of coregonids. Van Oosten (1929) illustrated a number of scales of lake herring from Lake Huron with marks between the annuli that I believe were accessory checks. Deason and Hile (1947) found that kiyis in Lake Michigan form definite annuli and prominent accessory checks on their scales despite small annual variation in water temperature (not over 2 or 3 degrees C) in the deep water where they live. Hile (1936) found that accessory checks occurred regularly on all scales of lake herring from Muskellunge Lake, Wisconsin, and Smith (1956) found false annuli on nearly all scales of Green Bay lake herring after the 2nd year of life. Barsukov (1960) described the annual formation of two rings on *Coregonus muksun*, a Russian whitefish.

Younger fish (ages 0–II) did not seem to form their accessory check earlier than older fish, although the check was more easily detected in young fish according to examinations of 10 marked fish and 34 unmarked fish. The clarity of the accessory check depended on the fish's growth rate after the check had formed. If the fish grew little after the late-October check formed on the scales, the check was faint and nearly indistinguishable on scales collected from November to January. If the fish did not grow after October, no scale material was deposited on the margin from November to March and an accessory check did not form. Of all the scales examined from marked fish, only three lake whitefish (larger than 400 mm, ages IV and V) and one bloater (241 mm, age II) failed to form an accessory check during 1 or more years.

GROWTH OF MARKED FISH

The marked fish grew fastest in the summer and slowest during the winter (Table II). The very largest fish in some groups showed no growth in length

TABLE II. Growth of various year-classes of marked fish in total length expressed as monthly percentage increases from annulus formation to annulus formation. Numbers of fish in parentheses; growth periods extend from the 16th day of one month to the 15th of the following month.

Period of growth	Lake whitefish 1958	Lake whitefish 1959	Lake whitefish 1962[a]	Bloater 1960	Bloater 1961	Kiyi 1961	Lake herring × bloater hybrid 1961	Avg
1962–63								
Mar.–Apr.	6.1(2)	7.8(1)	–	4.6(1)	13.8(1)	9.5(2)	7.1(3)	8.2
Apr.–May	14.1(2)	8.7(1)	–	8.6(1)	14.2(1)	11.9(2)	8.4(3)	11.0
May–June	16.2(2)	11.0(1)	–	9.6(1)	10.8(1)	12.4(1)	12.1(2)	12.2
June–July	22.1(2)	11.0(1)	–	10.4(1)	9.7(1)	10.5(2)	14.6(3)	13.1
July–Aug.	21.2(2)	11.0(1)	–	18.2(1)	9.3(1)	9.5(2)	13.3(3)	13.8
Aug.–Sept.	14.2(2)	9.7(1)	–	15.4(1)	14.0(1)	9.3(2)	11.6(3)	12.4
Sept.–Oct.	6.1(2)	9.2(1)	4.6(3)	14.4(1)	14.7(1)	11.0(2)	8.0(3)	9.7
Oct.–Nov.	0.0(2)	6.6(1)	4.9(3)	8.8(1)	7.8(1)	6.0(2)	3.2(3)	5.4
Nov.–Dec.	0.0(2)	5.7(2)	4.9(3)	5.8(3)	2.9(1)	3.2(1)	4.2(3)	3.9
Dec.–Jan.	0.0(1)	6.6(1)	5.0(3)	1.9(1)	2.8(1)	4.8(2)	4.5(3)	3.7
Jan.–Feb.	0.0(1)	6.5(1)	3.2(3)	0.0(1)	0.0(1)	5.5(2)	5.2(3)	2.9
Feb.–Mar.	0.0(1)	6.2(2)	3.0(3)	2.3(1)	0.0(1)	6.4(2)	7.8(2)	3.7
1963–64								
Mar.–Apr.	–	–	4.9(3)	–	3.6(1)	–	10.5(2)	6.3
Apr.–May	–	–	7.2(5)	–	8.4(1)	–	11.2(2)	8.9
June–July	–	–	12.4(3)	–	18.9(1)	–	16.8(1)	16.0
July–Aug.	–	–	15.7(3)	–	15.7(1)	–	16.6(1)	16.0
Aug.–Sept.	–	–	14.0(3)	–	13.6(1)	–	11.6(1)	13.1
Sept.–Oct.	–	–	8.7(3)	–	8.6(1)	–	8.1(1)	8.5
Oct.–Nov.	–	–	8.5(3)	–	6.1(1)	–	3.6(1)	6.1
Nov.–Dec.	–	–	6.8(2)	–	1.9(1)	–	1.7(1)	3.5
Dec.–Jan.	–	–	5.3(2)	–	0.0(1)	–	1.8(1)	2.4
Jan.–Feb.	–	–	2.9[b]	–	2.7(1)	–	1.7(1)	2.4
Feb.–Mar.	–	–	3.7[b]	–	3.7(1)	–	3.7[b]	3.7

[a] Percentages for periods of growth in 1962–63 were obtained by dividing the amount of growth of each period by the growth to the first annulus.

[b] Data were not available for these months — the figures used are averages for corresponding periods of the 1962–63 growing season.

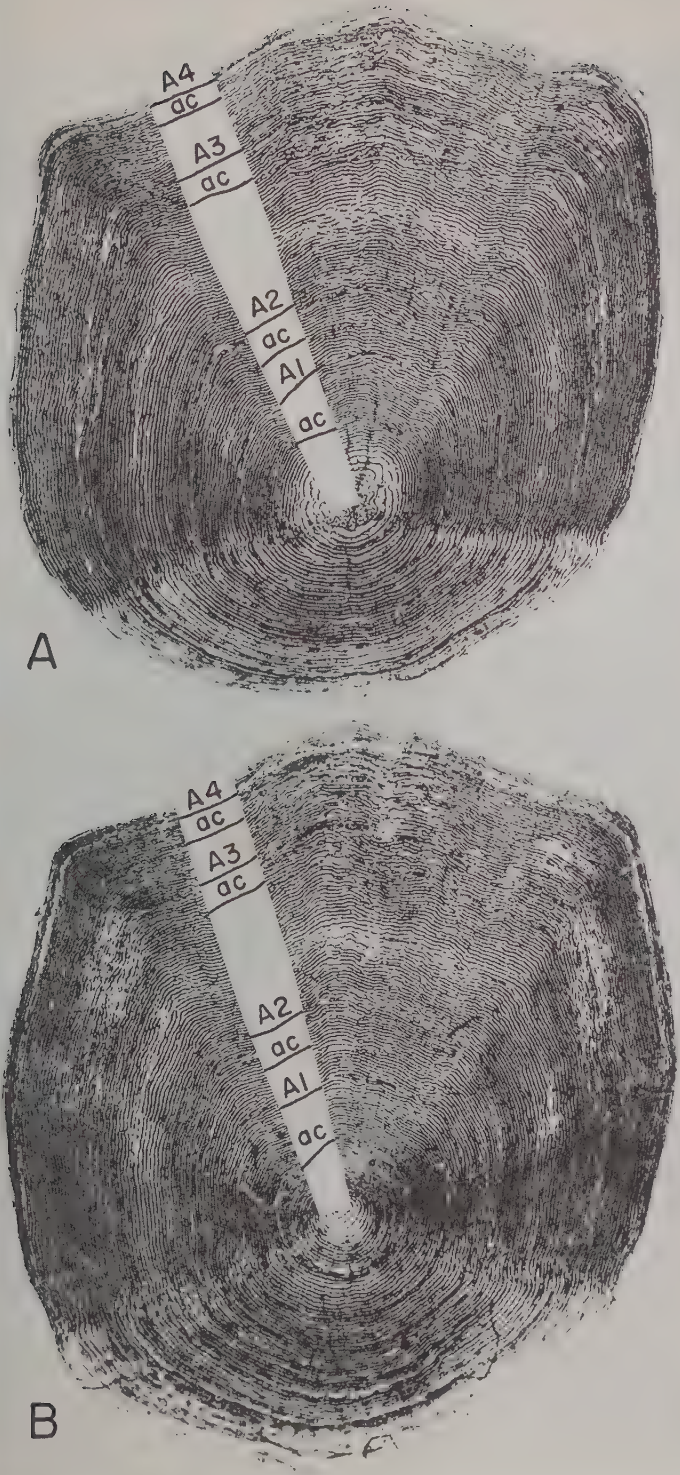
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FIG. 1. A, Scale taken from a lake whitefish (specimen no. 5, Table I) on April 2, 1963, showing annulus (A4) starting to form; previous annuli and accessory checks (*ac*) are indicated; total length 399 mm. B, Scale from same fish taken April 26, 1963, showing fourth annulus completely formed; total length 404 mm.

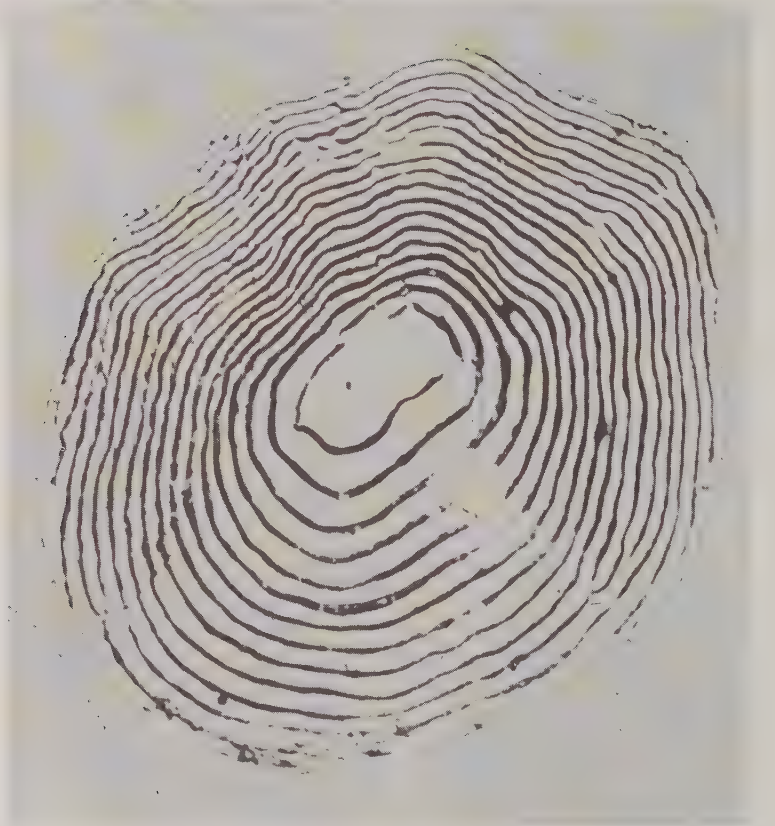

FIG. 2. Scale taken from a lake whitefish (specimen no. 2, Table I) on September 17, 1962, before accessory check had formed; total length 114 mm.

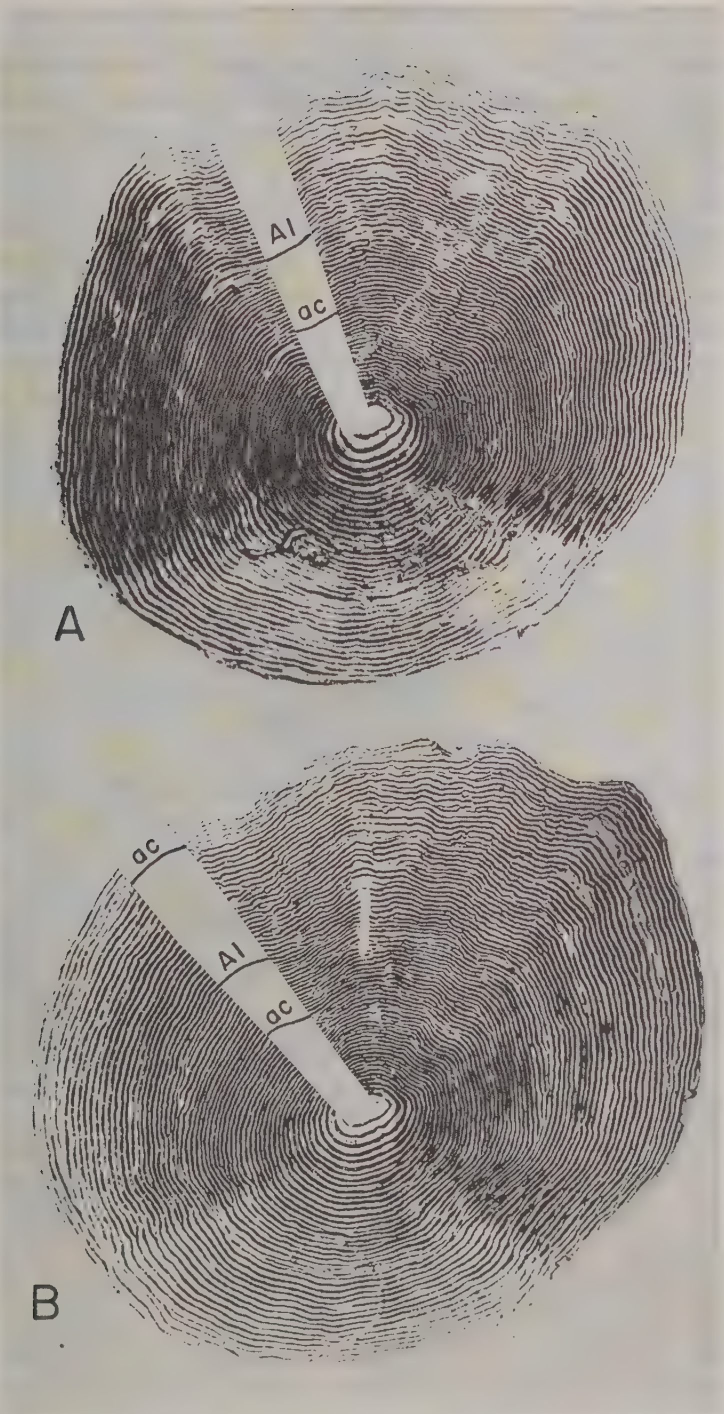

FIG. 3. A, Scale taken from a lake whitefish (specimen no. 2, Table I) on September 5, 1963, showing first accessory check and annulus; total length 246 mm. B, Scale from same fish taken on November 4, 1963, showing second accessory check completely formed; total length 264 mm.

or on the scales during the winter. All others grew throughout the year; the slow winter growth did not cause cessation of scale growth, nor in most of the fish studied was the formation of accessory checks preceded or accompanied by a period of greatly reduced growth or no growth.

Data for whitefish used to illustrate growth covered the period September 1962 to December 1963 (Fig. 4). The annuli were formed at the start of a period of more rapid growth or during constant growth, and accessory checks were formed after the growth rate had become slower. The bloater, kiyi, and hybrid had growth curves similar to but somewhat more irregular than those of the whitefish. The irregularities for these species were random and could not be correlated with annuli or accessory marks on their scales.

As the size of the fish increased the rate of growth decreased, as is typical for whitefishes (Carlander, 1950). Growth of mature lake whitefish and bloaters was negligible over the winter. Two whitefish of the 1958 year-class (specimens no. 6 and 7) that matured in 1962 at age IV did not grow after late fall, and a whitefish of the 1959 year-class (specimen no. 5) that matured at age IV

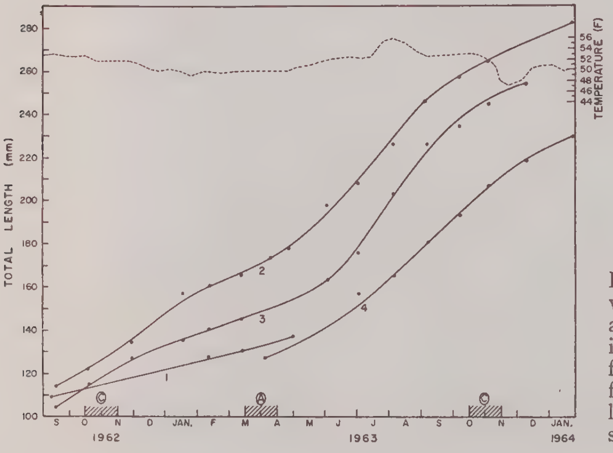

FIG. 4. Growth of four marked lake whitefish (1962 year-class) in 1962–64 and water temperature (broken line) in rearing tanks. Times of annulus formation (A) and accessory check formation (C) are indicated by circled letters. Numbers below curves are specimen numbers — see Table I.

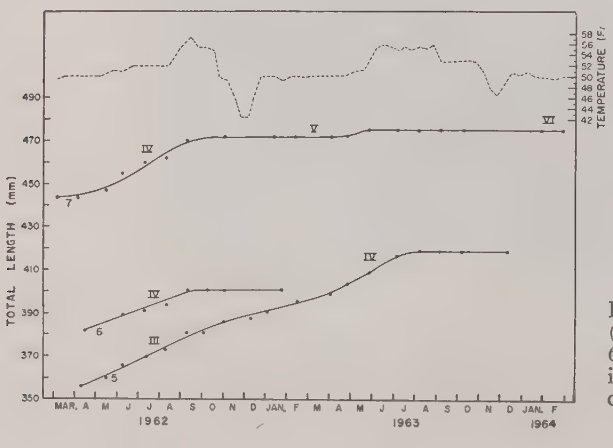

FIG. 5. Growth of lake whitefish (1958 and 1959 year-classes) in 1962–64 and water temperature (broken line in rearing tanks. Numbers below curves are specimen numbers — see Table I.

in 1963 did not grow after August 1963 (Fig. 5). The latter fish was growing at a nearly constant rate in March–May 1963 while its fourth annulus (Fig. 1) was forming.

BODY-SCALE RELATIONSHIP

None of the coregonids exhibited a constant body-scale ratio. The body-scale relationship for all species was described by a straight line; intercepts on the axis of length ranged from 34 to 46 mm. The relations between magnified (×41) scale diameter (S) and total length (L) in millimeters of marked and unmarked coregonids, year-classes combined, were:

Species	Equation
Lake whitefish	$L = 34 + 1.057\ S$
Bloater	$L = 46 + 1.003\ S$
Lake herring × bloater hybrid	$L = 36 + 1.041\ S$
Kiyi	$L = 34 + 0.947\ S$

Lengths were calculated from the formula:

$$L_n = a + \frac{(L_t - a)}{S_t} S_n$$

where L_n equals length of fish at annulus (or accessory check) n, L_t equals fish length at time of scale removal, a equals the total length intercept of the body-scale equation, S_t equals the total scale diameter, and S_n equals the scale diameter at annulus (or accessory check) n. The calculated length of a particular marked fish at annulus n agreed very closely (±1–3 mm) with its measured length when annulus n was formed, or with its measured length in March–April before the series of scale collections was started.

Although the length intercepts for lake whitefish, bloaters, and kiyi were entirely satisfactory for calculation of growth in my experimental stocks, I do not suggest that they are generally applicable. The body-scale relation is known to vary from population to population of the same species. In Lake Superior, for example, the body-scale regression for lake whitefish has an intercept on the length axis in the Munising Bay population (Edsall, 1960) but passes through the origin in the Apostle Islands stocks (Dryer, 1963).

EFFECTS OF TEMPERATURE, FOOD, AND LIGHT ON FORMATION OF ANNULUS AND ACCESSORY CHECK

The constancy of water temperature at 50 F (10.0 C) during time of annulus formation (Fig. 4 and 6) proves that changing temperatures were not necessary to initiate formation of an annulus on the scales. Van Oosten (1923) suggested that adult fish (age VIII and IX) stopped growing in the winter and that rising water temperature (from 39 to 45 F; 3.9 to 7.2 C) in March and April caused annulus formation on whitefish reared in the New

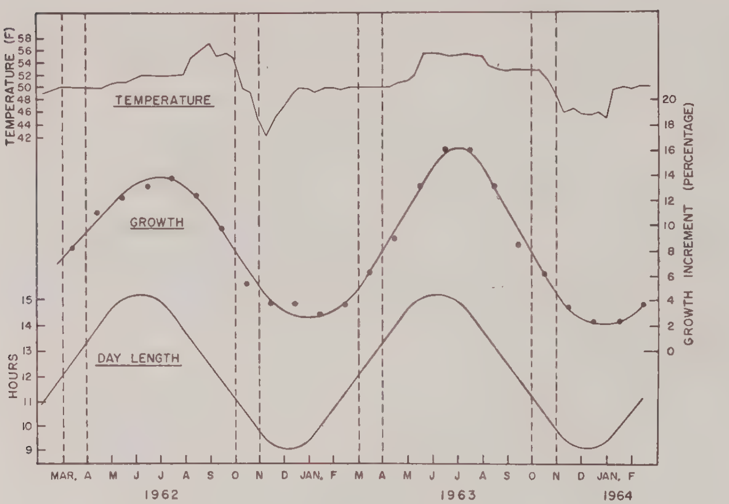

FIG. 6. Average monthly percentage increments of marked fish, hours of day length (sunrise to sunset), and average water temperatures, 1962–64. Periods of formation of annuli (March–April) and accessory checks (October–November) are indicated by vertical broken lines. Growth data from Table II.

York Aquarium. Only a few of the largest fish in the present study ceased growing during the winter.

During the period of accessory check formation, from mid-October to mid-November, water temperature decreased from 55.0 to 45.3 F (12.8–7.4 C) in 1962 and from 53.0 to 48.5 F (1.7–3.0 C) in 1963. The decrease during the same period was much less in 1958–61, however, and in some years it was less than 1 F (0.6 C): 53.6–51.2 F in 1958; 52.0–51.7 F in 1959; 52.8–52.0 F in 1960; and 51.9–49.4 F in 1961. Since all fish that were growing formed accessory checks in all years, it seems unlikely that temperature change alone may have caused formation of the accessory check.

In November 1962 and 1963 colder water from the holding pond was added to the water pumped into the tanks that held mature fish, to simulate water-temperature changes experienced by wild fish during the spawning period, but the changes (Fig. 5) came after the accessory checks had already formed. Cold water was not pumped into the tanks that held the immature fish of ages 0 and I (all species and year-classes). Consequently, they experienced less temperature variation in the fall (Fig. 4 for 1962); temperature did not fall below 49 F (9.4 C) for age 0, or 47 F (8.3 C) for age I. The use of spring water exclusively after the spawning period in mid-December kept the water temperature for all fish at 50 ± 0.3 F (10.0 ± 0.2 C) until late April or early May.

Neither the kind nor quantity of food was changed during the periods of formation of annuli and accessory checks, and no changes were observed in feeding during these periods. Mature whitefish ate less food during their spawning period, but spawning came after the check had formed. Mature whitefish shorter than 400 mm resumed normal feeding after spawning; those longer than 400 mm did not feed as actively.

Prophylactic inoculations of chloroamphenicol and sulfa drugs, administered monthly, could not be correlated with the formation of marks on scales.

Seasonal change in growth rate of the marked coregonids was much more closely related to day length (hours from sunrise to sunset) than to changes in water temperature (Fig. 6) or any other known factor. Monthly increments were lowest in late December to early February, when periods of daylight were shortest. The annulus did not begin to form until mid-March, when periods of daylight had started to lengthen. Separate growth curves for the marked whitefish of the 1962 year-class (Fig. 4) show more clearly the actual growth of most fish studied. The fall accessory check on the marked fish formed during a period of decreasing growth but the decrease was not sudden, nor was it followed by rapid growth after check formation.

The day length that coincided with the periods of mark formation was 12.1 hr in the spring and 11.0 hr in the fall. The fall mark formed 1–2 months before the minimum day length of 9.1 hr in late December and the annulus formed near the middle of the period of rapid increase in day length (Fig. 6). No attempt was made to control seasonal variations in light, or light in the tank room. The internal illumination from electric lights did not dominate the natural light entering the large windows surrounding the tank room.

AN EXPLANATION OF FORMATION OF MARKS

The formation of a spring mark during a period of increasing growth or small change in growth, and a fall mark during a period of declining growth or little change in growth is contrary to the usual assumption that a mark forms at the onset of rapid growth after a period of reduced or no growth. It has also been widely assumed that temperature, through its effect on a fish's metabolic rate, is the principal factor of annulus formation (e.g., Graham, 1928; Beckman, 1943; Lagler et al., 1962).

An increase in fish length may determine the increase in the scale diameter but the pattern of circuli may be governed by additional factors. Wallin (1957) discussed the development of scale markings in considerable detail. He showed that the circuli are caused by calcification of ridges produced by pressure of the scale against the scale pocket. The periphery of the scale is proteinaceous and subject to formation of pressure ridges. As additional protein is deposited around the scale, the ridges are farther from the edge and become impregnated with inorganic salts. A typical single ridge (or circulus) begins to form and is calcified along the anterior region (imbedded part of the scale), and then continues to form and calcify posteriorly around the lateral edges of the scale until the ends meet along the posterior margin. As many as 3–10 circuli can be in various stages of completion at one time. If protein deposition stops or is reduced the incomplete ridges calcify to their tips. Keeton (1965) demonstrated that the proteinaceous margin (Wallin's ossoid growth zone) may not become reduced when the rate of protein deposition is temporarily retarded or arrested, but the calcification of the ridges continues. If the proteinaceous growth resumes, the incomplete ridges do not resume their encircling growth, but a new ridge begins to form at the anterior edge, proceeds around the lateral edges, and eventually encircles the scale. This new ridge "cuts across" the incomplete circuli to complete the annulus characteristic of coregonids and many other fishes.

Possibly a physiological protein-demand cycle existed in the laboratory-reared coregonids that caused a periodic diversion of scale protein to support other metabolic functions. A biannual cycle would explain formation of annuli and accessory checks without a cessation in fish growth.

When coregonids become ripe in the fall, their gonad development may create a high protein demand. Many fish of the 1958 year-class that spawned in 1962 and 1963 showed evidence of scale resorption in late summer and fall, which suggests the diversion of scale protein. Immature fish did not show scale resorption in the fall but apparently experienced a sufficient change in their protein-deposition rate to form the characteristic accessory check.

The formation of an annulus in the spring may also reflect a metabolic change during the period that growth was increasing or nearly constant, but the reasons are unknown. Conceivably, the demand could be generated by increased activity during the time of rapidly lengthening days.

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RATES OF RESPIRATION OF ESTUARINE FISH [1]

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ABSTRACT

A flowing-water respirometer was used to measure oxygen consumption of five species of estuarine fish: pinfish, *Lagodon rhomboides*; black sea bass, *Centropristes striatus*; Atlantic croaker, *Micropogon undulatus*; oyster toadfish, *Opsanus tau*; and mummichog, *Fundulus heteroclitus*. The relation between the amount of oxygen consumed and body size, in general, may be expressed by the formula $Q = a \text{ Weight}^k$, where a and k are constants derived from experimental data for a species. Some investigators have stated that k values do not vary significantly among species of fish. In my investigations the value of k did vary significantly between certain species. The values obtained for k are given and the methods used to measure respiration rates are discussed.

INTRODUCTION

The rates of respiration of fish and the relation between these rates and the weight of the fish have been used to calculate energy requirements of populations of fish. Respiration is generally related to body weight by the equation $Q = aW^k$ where Q is the respiration rate or routine metabolism (Beamish and Mookherjii, 1964), a and k are constants for the species, and W is the weight of the fish. Some question concerning this relation exists, however. Winberg (1956) implied that respiration rate and weight are linearly related throughout life but Hickman (1959) believed that the relation changes with the development of the fish.

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Extensive data on rates of respiration of many species of fish, predominantly fresh water, have been compiled by Winberg (1956). From these data (which were collected by many investigators using different methods), he calculated a basic equation ($Q = 0.3W^{0.8}$) to use as a first approximation of the relation between weight and metabolism in fish. The assumption is made that the relation between weight and metabolism is linear (double logarithmic plot) and does not change during ontogeny of the species. A modification of Winberg's equation was used to measure the energy requirements of a population of fish in a river (Mann, 1965). According to Mann, evidence is abundant that Winberg's value of 0.8 for k is correct, but that the value of a may vary over a considerable range for different species. Calculated regression lines for several species of fish, therefore, would have the same slope (k) but not necessarily the same intercept (a). Thus, Mann has recommended using a fixed slope of 0.8 and calculating the value of a from the empirical data.

The purpose of my experiments was to determine whether Winberg's basic equation or Mann's modification describes the relation between oxygen consumption and weight in selected species of estuarine fish of the Beaufort, N. C. area.

METHODS AND MATERIALS

Fish used in these experiments were collected near Beaufort, N. C., and maintained in tanks in the laboratory before their rates of respiration were measured. The species were: pinfish, *Lagodon rhomboides*; black sea bass, *Centropristes striatus*; Atlantic croaker, *Micropogon undulatus*; oyster toadfish, *Opsanus tau*; and mummichog, *Fundulus heteroclitus*.

Oxygen consumption was measured in a recirculating water system which was a modification of that used by Keys (1936) and by other investigators (Figure 1). Although this system was designed to recirculate the water it could easily be converted to a single pass system, depending on the needs of the investigator. The system consisted of a reservoir, respirometer tank, constant-level tank, and respiration chambers constructed of plastic. Water from the reservoir was pumped into the elevated constant level tank and then flowed by gravity to each respiration chamber; the excess water from the chamber returned through the overflow to the reservoir. Water flowing from the respiration chamber also returned to the reservoir. The rate of flow of water through each respiration chamber was regulated by adjusting the height of the plastic tube leaving the chamber (Figure 1) and was measured by diverting the flow from the chamber into a graduated cylinder for specific intervals of time. Rate of flow was measured just before water samples were analyzed for oxygen content with an oxygen meter. The water was maintained at 20° ± 1° C. and saturated with oxygen. Sea water of 33 ± 1 °/00 salinity was used in all experiments. The test fish were not fed for two days before an experiment and were acclimated to the respiration chamber for 24 hours before the first oxygen sample was taken.

COMPARISON OF RESPIRATION RATES

Knowledge of the metabolism of organisms may be used to estimate their food or energy requirements in ecological field studies. An estimation of metabolism may be obtained by measuring the oxygen consumption of fish. Regression coefficients for the relation between metabolism and weight can be calculated on the basis of oxygen consumption and weight of the fish. There are two possible interpretations of this relation between metabolism and weight (Winberg, 1956). One is that the values for a and k obtained from the experiments are typical for all fish, and indicates a general relation between metabolism and weights; the other is that metabolism varies with size in different species. Winberg concluded that, in general, the first interpretation is correct and that usually the relation between total metabolism and weight may be approximated by the equation $Q = 0.3W^{0.8}$. Mann (1965) agreed that

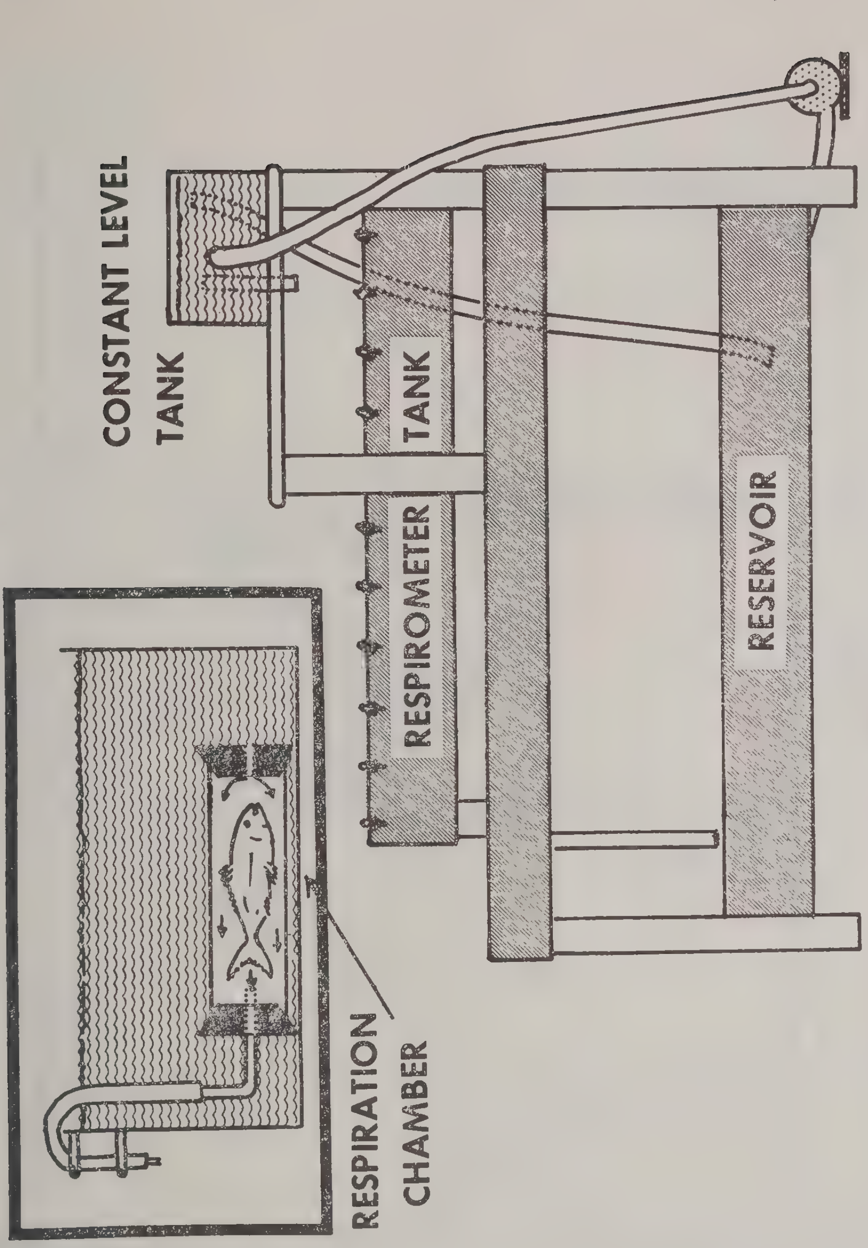

Figure 1. Recirculating water system used to measure respiration in fish. The insert is a transverse section through one of the 10 respiration chambers.

the slope of the regression line (k) would be near 0.8 but stated that the intercept (a) varies among species and should be calculated from the empirical data and a fixed k value of 0.8.

In these experiments, both Winberg's and Mann's methods were used to calculate regression lines for the experimental data. These lines were then compared with the regression line calculated by the least-squares method from the data obtained in this study. For each species of fish, the mean rate of oxygen consumption was plotted against total body weight on a double logarithmic scale (Figures 2 and 3).

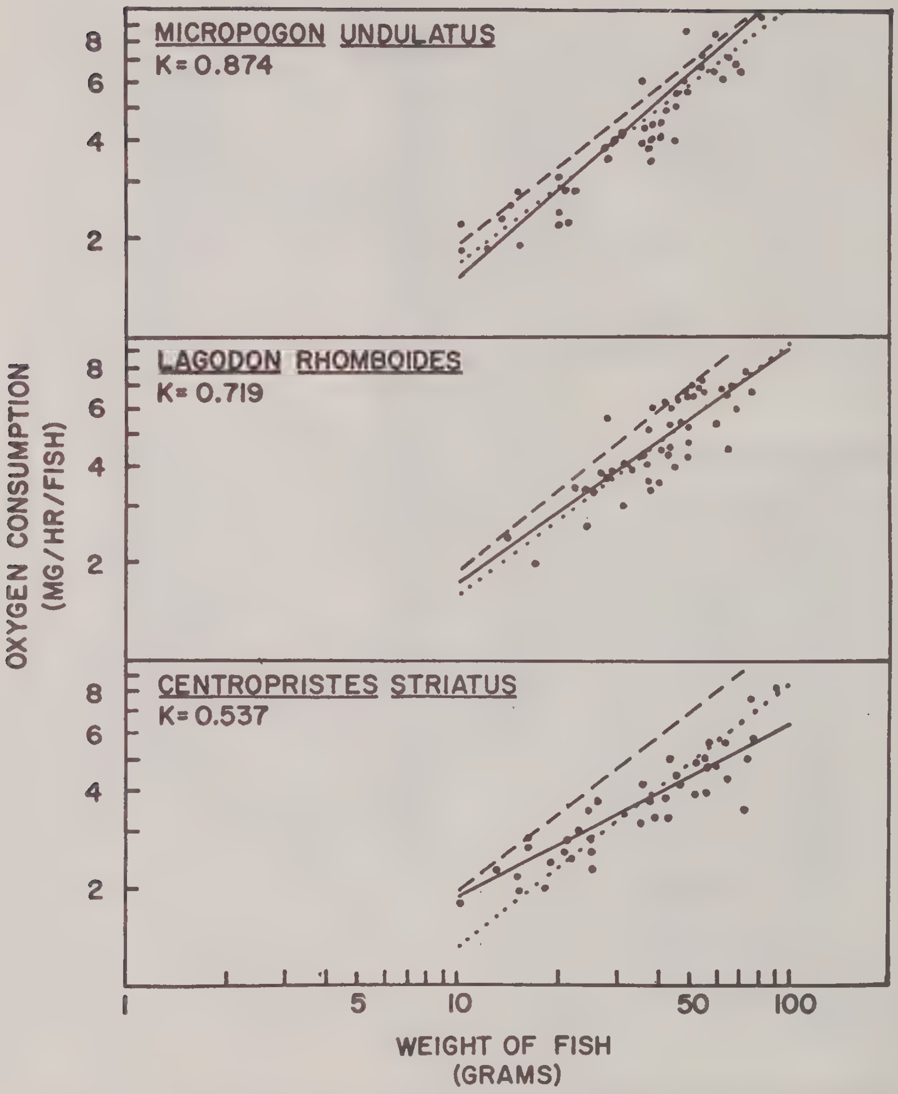

Figure 2. The effect of weight on rate of respiration of Atlantic croaker, pinfish, and black sea bass. The solid line is the calculated regression line, the broken line is from Winberg's basic equation, and the dotted line is from Mann's modification. Each point represents the mean of five measurements on a single fish.

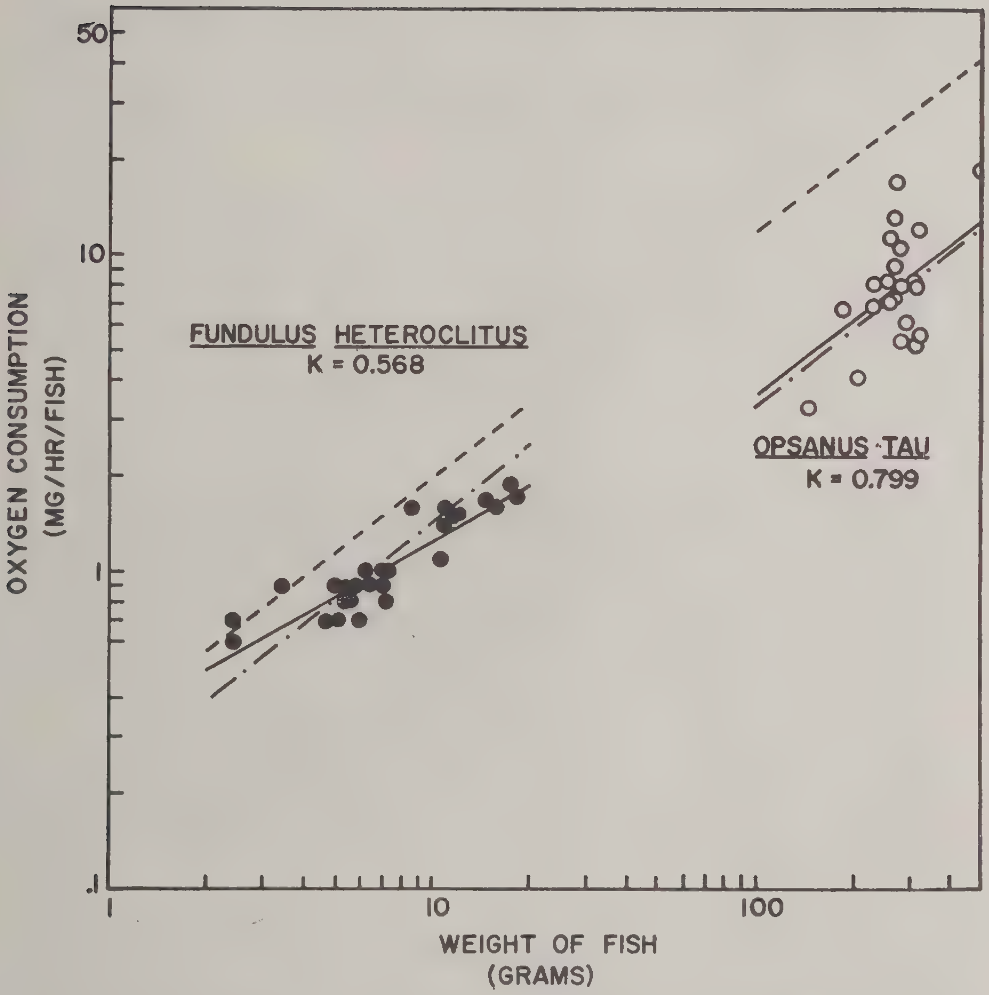

Figure 3. The effect of weight on rate of respiration of mummichog and toadfish. The solid line is the calculated regression line, the broken line is from Winberg's basic equation, and the dotted line is from Mann's modification. Each point represents the mean of five measurements on a single fish.

The slope (k) of the regression line for each species of fish was less than unity; oxygen consumption per unit weight thus is greater for smaller than for the larger fish (Table 1). This finding is in general agreement with reports (Beamish 1963, Hickman 1959, Winberg 1956) on other species of fish which showed, with few exceptions, that oxygen consumption per gram decreased with increased weight. The k values ranged from 0.874 (croaker) to 0.537 (black sea bass). The calculated k values for croaker, pinfish, and toadfish are only slightly different from the value calculated by Winberg. The slopes of the lines for black sea bass and mummichog, however, differed considerably from Winberg's basic equation. The difference in number of fish of each species examined, size distribution, and relatively high individual variation of oxygen consumption made statistical comparison of respiration differences difficult. Also, as pointed out by Hickman (1959), fish in different stages of development cannot be compared. For example, a 10 g. mummichog would be considered a mature fish and not comparable to a 10 g. juvenile toadfish. Statistical comparisons, therefore, were made only among black sea bass, pinfish, and croaker, since a substantial number of fish (Table 1) over a comparable size range (10 to 100 g.) were available for these three species.

TABLE 1 — SUMMARY OF OXYGEN CONSUMPTION EXPERIMENTS ON FIVE FISHES OF THE BEAUFORT, N. C. AREA

Species	Number of fish	Weight range (grams)	a	k	Standard error of k
Micropogon undulatus	42	10-80	0.198	0.874	0.066
Lagodon rhomboides	46	13-74	0.335	0.719	0.072
Centropristes striatus	41	10-72	0.536	0.537	0.045
Fundulus heteroclitus	27	2-18	0.339	0.568	0.054
Opsanus tau	21	150-500	0.092	0.799	0.320

The calculated regression line for each species extrapolated to 1 g. is shown in Figure 4. The data were tested by analysis of covariance to determine whether a true difference existed between the slope of the three regression lines. The hypothesis that the three lines are parallel was rejected at the 0.01 probability level, indicating that the relation between metabolism and weight is not the same for all three species of fish.

The most accurate estimate of a and k for each species was obtained from regression lines calculated from the experimental data. Neither Winberg's basic equation nor Mann's modification gave satisfactory regression lines for all five fish, but Mann's method gave results that were consistently closer to the calculated regression line than Winberg's (Figures 2 and 3). In the experiments where it was possible to compare respiration in three species of fish at about the same stage of development (Figure 4), a statistical difference among the slopes of the three regression lines was demonstrated. This difference indicates that metabolism does vary with size among the species examined, and therefore one equation will not describe the relation between metabolism and weight for all species of fish.

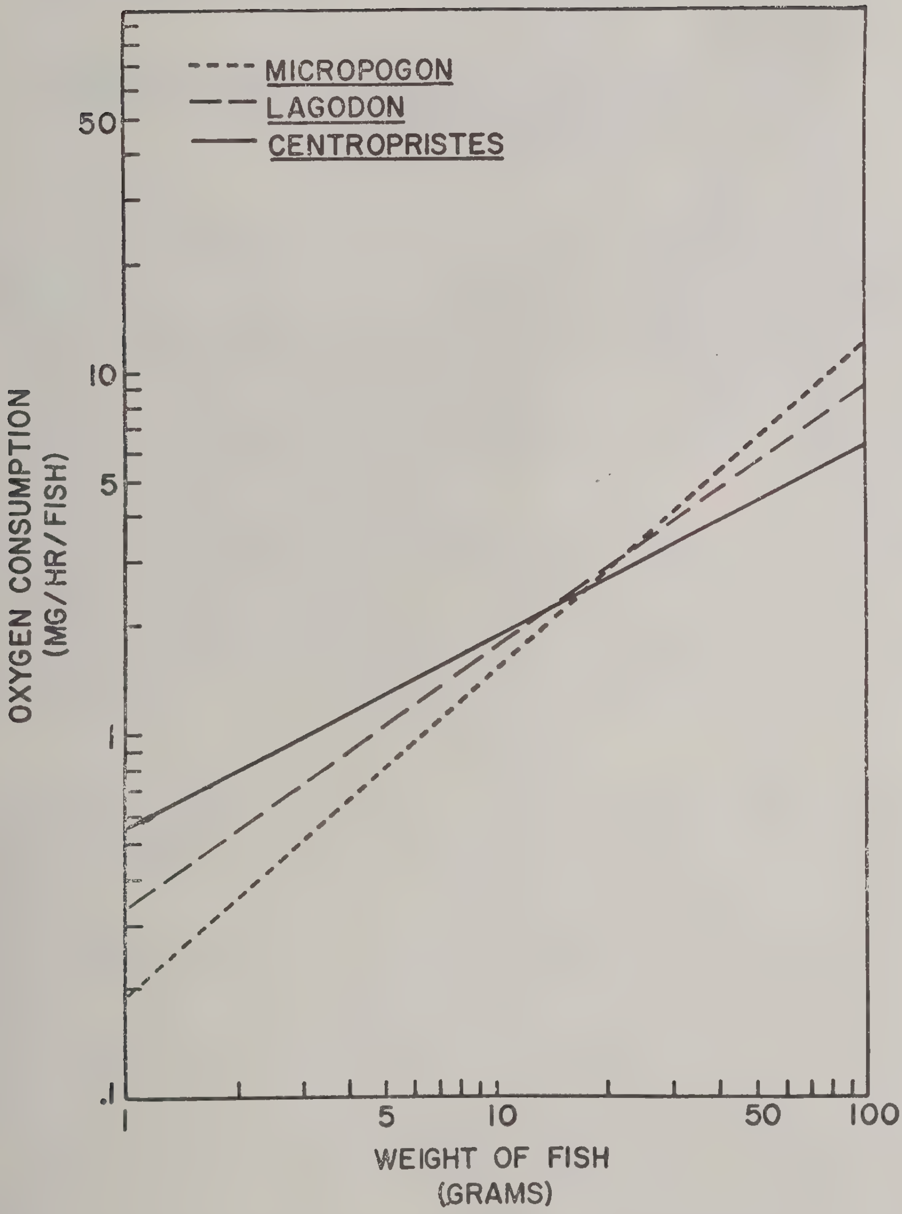

Figure 4. A comparison of the regression of oxygen consumption on weight for Atlantic croaker, pinfish, and black sea bass.

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Effects of Light on Schooling and Feeding of Jack Mackerel, *Trachurus symmetricus*[1]

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ABSTRACT

Schools of six jack mackerel each were photographed with infrared film at eight levels of luminance and also in darkness. Three indices were used to measure the behavior of the school from motion pictures. Two of the indices, mean distance to nearest neighbor and mean separation distance, were measures of the distances between individuals in a school; the other, mean angular deviation, was a measure of differences in orientation between individuals. A value for each index was calculated for each motion picture frame.

From 12.1 to 6×10^{-6} ft-L no differences existed in the angular deviation of the school or in the distances between fish. At 6×10^{-7} ft-L the intervals between fish were much larger than at higher levels of brightness and groups showed little uniformity in their orientation. Below 6×10^{-7} ft-L (darkness) schools were dispersed and the distributions of values of angular deviation were random.

The ability of jack mackerel to feed on live adult *Artemia* was also tested at eight levels of luminance and in darkness. The number of *Artemia* eaten at 6×10^{-5} ft-L was about half of that eaten at the normal daytime level of 12.1 ft-L. Few *Artemia* were eaten at 6×10^{-7} ft-L and none in darkness.

Comparison of these data with measurements of light in the sea indicated that jack mackerel probably would be able to maintain schools near the surface on a moonless starlit night and that they probably could feed effectively near the surface on a full moonlight night.

INTRODUCTION

The dominant modality involved in the formation and maintenance of fish schools is vision (Atz, 1953; Breder, 1959). All species studied at the time of Atz's (1953) review of schooling behavior were reported to be unable to maintain a school in darkness. No measurements of illumination were made in these studies; thus, the level of illumination at which schooling ceases is of interest and has been the object of a number of investigations (see reviews by Shaw, 1961 and Blaxter, 1964). A wide range of visual thresholds for schooling exists from 5×10^{-2} ft-c for *Menidia* (Shaw, 1961) to 1×10^{-6} ft-c for *Astyanax* (John, 1964). John (1964) pointed out that the reported variations in visual threshold for schooling probably are as much the results of arbitrary definitions of schooling and photometric errors as they are variations among species.

In this paper I have related the schooling behavior of juvenile jack mackerel, *Trachurus symmetricus* (Ayres), to the photometric brightness or luminance in an experimental tank. I have also included data on the effect of different levels of luminance on feeding behavior to provide additional information on the relation between light and the behavior of jack mackerel.

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To avoid as many photometric errors as possible, room, tank, and light sources were designed to provide a diffuse illumination and a field of uniform luminance. Luminance in the tank was changed without altering the spectral composition of the light and photometric measurements were made within the tank.

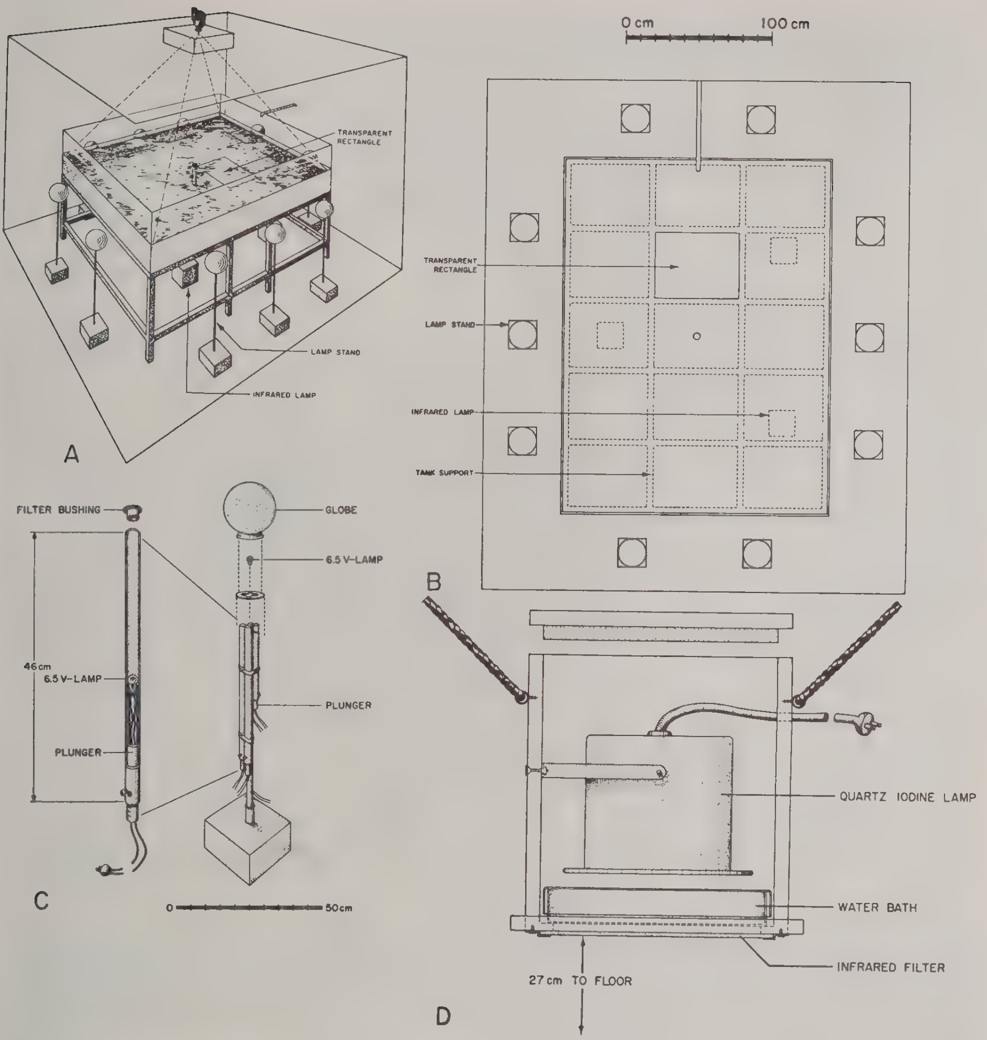
APPARATUS AND GENERAL METHODS

The facilities consisted of a concrete block room constructed on a foundation separate from the rest of the experimental aquarium at the Fishery-Oceanography Center, La Jolla, Calif. The room was light-tight and was supplied with fresh circulating seawater. The floor, walls, ceiling, and all structures in the room were painted with flat white paint of high reflectivity (photometric sphere paint). The lens of a 16-mm time-lapse movie camera was placed in a port in the ceiling of the room above a plexiglass tank, 183 × 244 × 52 cm, constructed in the same relative dimensions as a 16-mm motion picture frame (Fig. 1A and B). The inside surfaces of the bottom and the sides of the tank were sprayed up to the waterline (18 cm) with a white acrylic paint. A rectangle on the bottom of the tank (61 × 49 cm) was left unpainted so that photometric measurements could be made from beneath the tank. During an experiment this transparent window was covered by a piece of white plexiglass of about the same transmittance as the painted bottom.

The room was illuminated by 10 fixtures (Fig. 1C) spaced at regular intervals around the perimeter of the tank. Each fixture supported five No. 81, 6.5-v, 2885 Kelvin lamps; four of the lamps were attached to the upper ends of plungers which were inserted inside tubes lined with black velour casket cloth; and one lamp was fixed and not enclosed in a tube. A bushing which contained a disk of white plexiglass and often a neutral density filter was inserted into the end of each of the tubes. The upper ends of the tubes were enclosed by a globe of white opal glass.

Only 10 lamps (1 per fixture) were on at any one time; different lamps in the fixture were used to produce different levels of luminance within the tank. The output of each adjustable lamp was changed by moving the plunger and by changing neutral density filters. The fixed, non-adjustable lamps produced the normal day luminance; the adjustable lamps produced lower test levels of luminance. Variation in luminance among lamps did not exceed 10%.

Kodak high-speed infrared film was used to photograph the fish. Infrared radiation was obtained from three 250-w, 3400 Kelvin quartz iodine lamps (Fig. 1D) suspended beneath the tank facing the floor. Mounted under each lamp was a water bath and a Corning 7-69 filter which transmitted infrared radiation and absorbed visible radiation. This system provided adequate infrared photographs of fish schools. Figure 2 shows that sources of infrared radiation much below 3400 K would be inefficient and that photography would be difficult in water deeper than 50 cm. Infrared photography of fish and other aquatic organisms has been discussed in detail by Duncan (1956) and Baylor (1959).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PLUNGER
PLUNGER
C
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50 cm
QUARTZ IODINE LAMP
WATER BATH
INFRARED FILTER
27 cm TO FLOOR
D

Fig. 1. Apparatus used to determine the effects of luminance on schooling and feeding behavior of jack mackerel. A, three dimensional drawing of room and tank; B, orthographic scale drawing of tank and room; C, detail of lamp stand; and D, detail of infrared lamp used for photographic illumination.

During any experiment the infrared lamps were kept on for 0.8 sec of each minute while a photograph was taken. Although the fish might have been capable of using the infrared radiation, the infrared lamps were on for such short periods that it seems doubtful that any error was introduced.

Photometric Units

The behavior of jack mackerel was studied in relation to luminance (photometric brightness) in the tank rather than to illuminance (light intensity). The luminance of a surface in foot-Lamberts is equal to the product of its

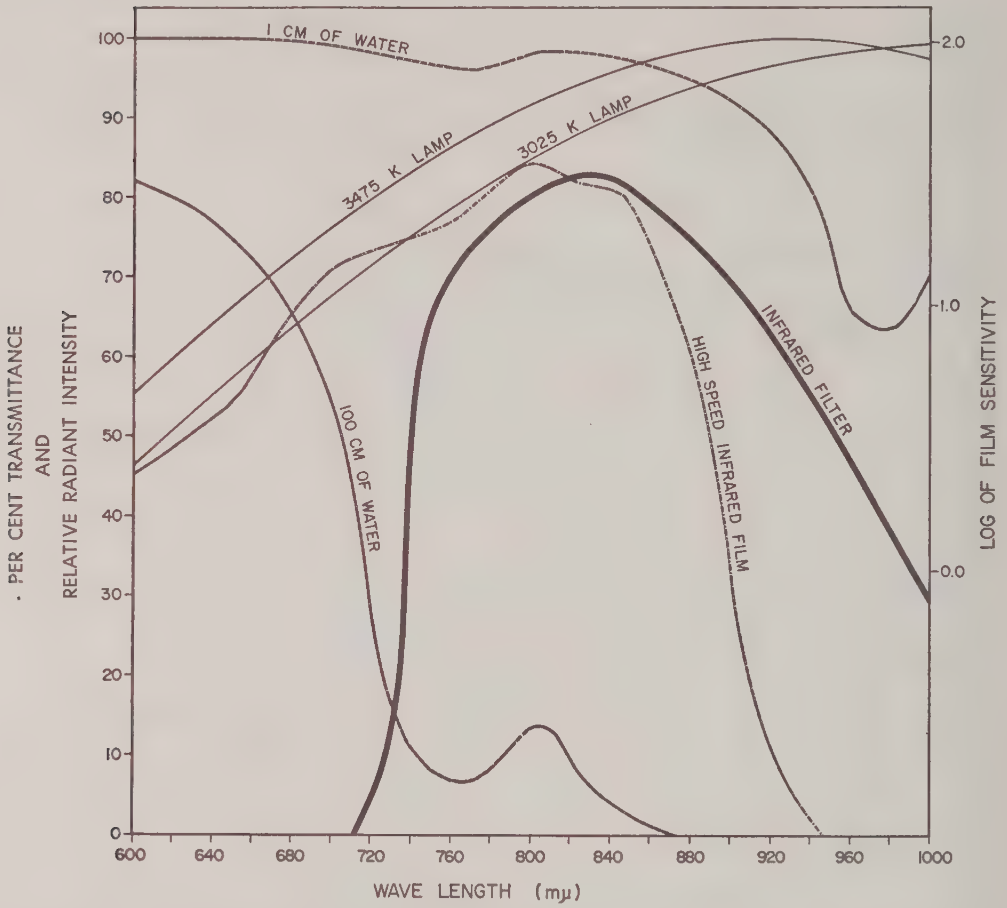

FIG. 2. Relation of the spectral sensitivity of high speed infrared film to: the spectral transmittance of the infrared transmitting filter (manufacturer's specifications); the spectral transmission of light through 1 and 100 cm of water (from Withrow and Withrow, 1956); and the relative spectral irradiance of tungsten lamps of 3025 and 3475 K (from Withrow and Withrow, 1956).

luminous directional reflectance multiplied by its illuminance in foot-candles. In all previous studies of light and schooling, measurements of illuminance were used rather than luminance. The luminance of surfaces in the path of sight is a better measure of the adaptive state of the eye than are measurements of the downwelling illuminance; for example, two containers that received equal illuminance could produce different adaptive states if the reflectances of the surfaces within the containers differed (Duntley, 1960).

It is impractical to convert the photometric measurements of intensity reported in the literature to luminance because the reflectivities of the environments are unknown. The containers varied widely: some were of concrete, others were of glass, and some had opaque white walls. Such differences in tank types might easily produce marked differences in the adaptive state of the eye even though the illuminances entering the tanks were equal. Thus, for rough comparisons of my data with values in the literature, it seems preferable to consider the foot-candle measurements made in previous studies to be equivalent to the foot-Lambert measurements made here. It should be kept in mind, however, that in the same environment these two units would be equal only if the surfaces reflected light perfectly.

Photometric Procedures

A Gamma Scientific 700 log linear photometer provided with a 931A photomultiplier and a 180° cosine collector was used to measure levels of luminance in the tank. The photometer was calibrated in absolute units with a Gamma Scientific luminance standard, 100 ft-L at 2854 ± 50 K. A photopic filter was inserted in the optical path of the receptor to adjust the response of the 931A photomultiplier to the standard luminosity curve.

Measurements were made through the bottom of the tank at the unpainted window or within the tank 6 cm below the water surface. Measurements made through the bottom were multiplied by a constant to make them equal to those made within the tank. Each neutral density filter or combination of filters used in the calibration was calibrated on an optical bench. The luminance within the tank was measured each time a test was conducted.

Manufacturer's specifications indicated an accuracy characteristic of the photometer of ±2% when the instrument was calibrated against the luminance standard. Considering all sources of error during the calibration process, the error for most levels was ±10%. At 6×10^{-7} ft-L the error increased to ±15–20% because a higher voltage setting was used (1110 v) and the instrument was less stable.

Measurements were also made with a receptor which had a 2° acceptance angle to determine the extent of variability in luminance within the tank. The receptor was rotated on its axis under water, and readings were made at 5–10° intervals. An example of these readings is shown in Fig. 3, where the set of values at 6×10^{-1} ft-L was plotted on tracings of two underwater photographs taken with a camera which had a 180° lens. Thus, each field of view shown in the illustration resembles that seen through one eye of a fish. Photographs were also taken of a jack mackerel in the tank and the relative luminance of the fish was calculated from the optical density of the image.

Luminance within the tank did not vary greatly. The least bright area in the fish's field of view, parts of the bottom directly above the tank supports, were only 29% darker than the brightest region, the ceiling of the room as viewed by a fish through its window in the water surface as described by Walls (1942). The fish was darker than its background; the darkest areas of the body were the darkly pigmented back and the pupil and the brightest were the silvery sides and belly. The pupil had the greatest contrast with the background.

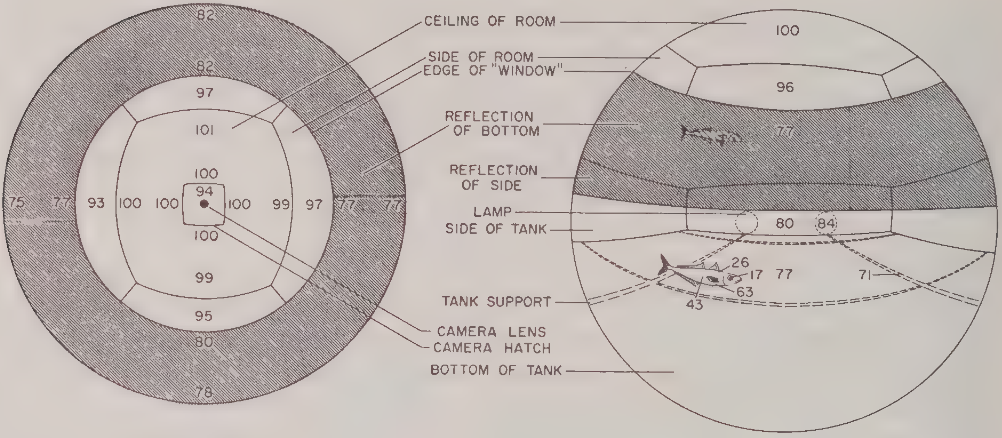

FIG. 3. Distribution of luminance viewed from within experimental tank at 6×10^{-1} ft-L. Simulations of view by a fish eye were made with a 180° "fisheye" lens. *Left panel*, hemispherical projection of visual field if path of sight is directed upward from bottom; hatched area is reflection of bottom on the silvery underside of water surface; and area within inner circle is portion of room visible through the "window" in the water surface. *Right panel*, hemispherical projection of visual field if path of sight is directed toward one end of tank from the center; circles of broken lines indicate positions of lamps outside tank wall; bands of broken lines indicate positions of supports beneath tank bottom.

LIGHT AND SCHOOLING

METHODS

Four groups of six jack mackerel each were tested at nine levels of luminance: 6×10^{-7}, 6×10^{-6}, 6×10^{-5}, 6×10^{-4}, 6×10^{-3}, 6×10^{-2}, and 6×10^{-1} ft-L, daylight (12.1 ft-L), and darkness (an unknown level of luminance below the sensitivity of the photometer). The length of the fish ranged from 105 to 141 mm standard length and the temperature in the tank varied from 17.2 to 21.0 C.

Each group was placed in the experimental tank 3 days before its first test. The daily light schedule in the tank during the acclimation period was: 0900–1000 hr, 13.5×10^{-2} ft-L; 1000–1800 hr, 12.1 ft-L; 1800–1900 hr, 13.5×10^{-2} ft-L; and 1900–0900 hr, darkness. The fish were fed frozen adult brine shrimp at 1200–1300 hr daily and the tank was cleaned at 1500–1600 hr. This schedule was continued after the tests started except that one of the test levels of luminance was substituted for 13.5×10^{-2} ft-L at 0900 hr. Only one level of luminance was tested per day, the order of the tests was random, and groups were tested only once at each level. Groups remained in the tank 12–20 days.

During each test single infrared photographs were taken at 1-min intervals from 0800 to 1100 hr. This schedule provided a photographic record of the activities of each group for 1 hr in the dark, 0800–0900 hr; for 1 hr at a randomly determined test level of luminance, 0900–1000 hr; and for 1 hr at the daytime luminance of 12.1 ft-L, 1000–1100 hr. Usually the photographs of the first 50 min of each of the three 1-hr periods were analyzed. Occasionally, some of the first 50 frames had to be discarded because of poor picture quality and the analysis was extended to include an equal number of frames from the remaining 10 min of a 1-hr photographic sequence.

Three indices of schooling behavior were calculated from each frame: *mean separation distance*, the average of the horizontal distances separating each fish from every other fish in the school; *mean distance to the nearest neighbor*, the average of the horizontal distances from each fish in a school to its nearest neighbor; and *mean angular deviation*, the average number of degrees each fish deviated from the resultant direction of the group. The first two, mean separation distance and mean distance to the nearest neighbor, are measurements of the compactness of a school; the last, mean angular deviation, measures the angular differences in heading among individuals in a school. These indices permitted an objective evaluation of changes in schools independent of definitions of schooling behavior. The limitation, and details of calculation, of the indices have been described by Hunter (1966). Indices of schooling similar to these and which also take into account movements in the vertical plane have been developed by Dambach (1963) and Cullen et al. (1965).

Spacing and Angular Deviation of Schools

In darkness no schooling occurred. The orientation of the groups was random; no difference ($P < 0.05$) existed between the mean angular deviation of any group in darkness and the one calculated for 1 million randomly determined angles for six fish (Kolmogrov-Smirnow one sample test, Siegle, 1956). The median of all values of mean angular deviation in darkness (Fig. 4) was the same in each group as the median for the random distribution, 64°. In darkness the fish were widely distributed; the mean distance to nearest neighbor and mean separation distance in the dark were always higher than they were under brighter conditions (Fig. 5, 6). Groupings larger than pairs were rare in the photographs taken in the dark, and even pairs were so infrequent that their occurrences probably were by chance.

At 6×10^{-7} ft-L the three indices of schooling were different ($P < 0.01$) from those recorded in darkness: the mean angular deviations of groups 1, 2, and 3 differed from the random distribution; the mean separation distances of all groups differed from those of the preceding dark period; and the mean distances to nearest neighbor of groups 1, 3, and 4 differed from those of the preceding dark period. At 6×10^{-7} ft-L fish did not maintain groupings consistently and did not respond immediately to the increase in luminance. For example, in group 1 the distribution of fish during the first 15 min of the test period resembled that in darkness; no grouping larger than a single pair of fish was photographed. During the next 35 min, a grouping of three fish, then one of five, and then another of five formed and dispersed.

At 6×10^{-6} ft-L, 1 min after the lights were turned on, groupings were formed in which the distances between individuals were less than those in the dark. Within 3–4 min after the lights were turned on the fish had formed a compact, discrete school, in which the distances between fish were small and the orientations of individuals was non-random and did not vary greatly. No changes occurred during the rest of the test.

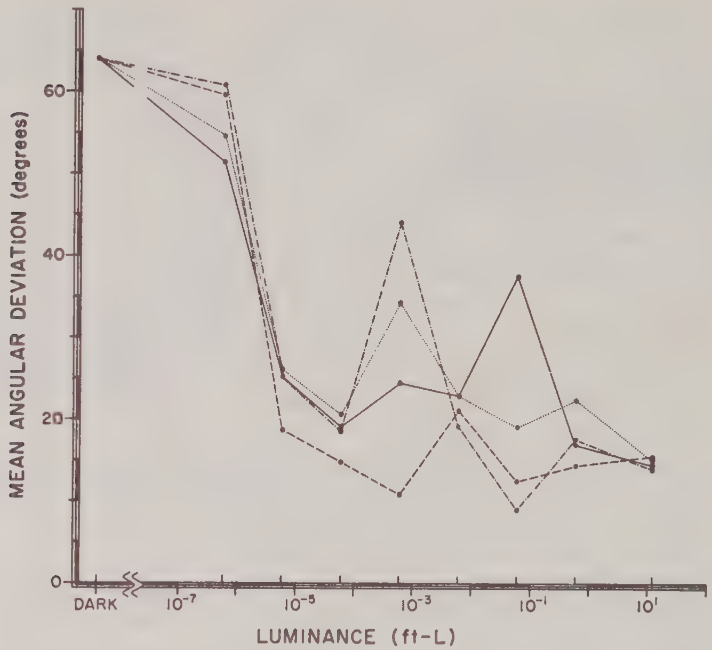

FIG. 4. Relation between luminance (logarithmic scale) and mean angular deviations of four groups of jack mackerel. Marks above abscissa indicate positions of data points; marks below indicate logarithmic scale. Points are medians of 50 values of mean regular deviation; lines connect the medians for each group.

Thus, within an increase of one order of magnitude of luminance, at the relatively low levels 6×10^{-7} to 6×10^{-6} ft-L, the schooling response of jack mackerel changed from one in which groupings of various sizes were maintained for short periods to one in which all fish remained in a compact school throughout a 1-hr period. At higher test levels of luminance (e.g. 6×10^{-1} ft-L) schools were essentially the same as those formed at 6×10^{-6}.

From 6×10^{-6} to 6×10^{-1} ft-L the distances between fish (Fig. 5, 6) were the same, but the angular deviations of the schools at 6×10^{-4} and 6×10^{-2} (Fig. 4) were variable. The reason for the increased variability of the angular deviation of schools at these two levels of luminance is unknown. It may be related to a shift from scotopic to photopic vision which may occur within this range.

In all groups, the medians for mean separation distance and mean distance to nearest neighbor were higher in the daylight sequence than in the preceding sequence ($P < 0.05$). That the distances between fish increased in daylight may have been the result of food deprivation. Hunter (1966) demonstrated that the distances between fish in jack mackerel schools increased with food deprivation.

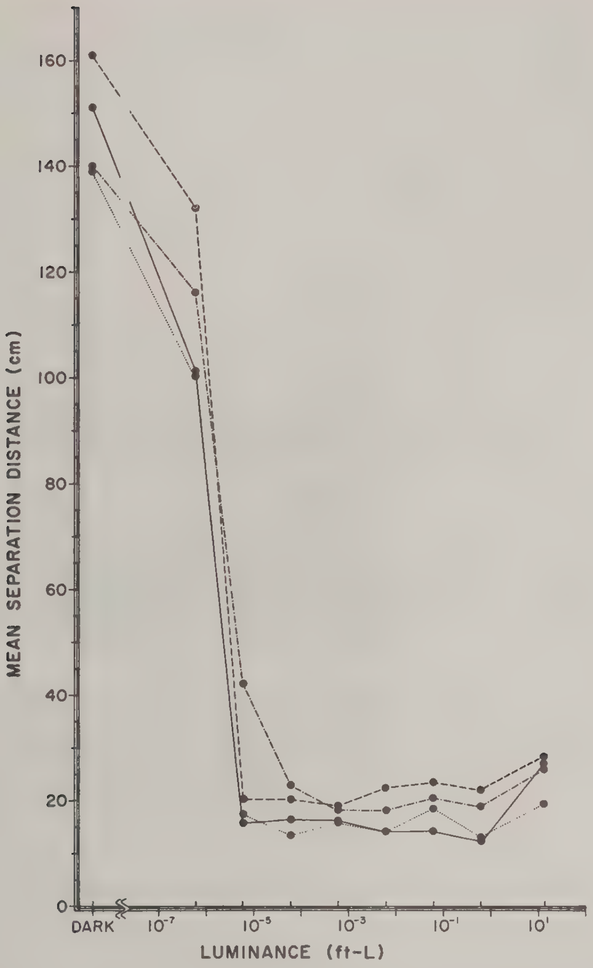

FIG. 5. Relation beween luminance (logarithmic scale) and mean separation distances of four groups of jack mackerel at various levels of luminance. Marks above abscissa indicate positions of data points; marks below indicate logarithmic scale. Points are medians of 50 values of mean separation distance; lines connect the medians for each group.

LIGHT AND FEEDING

The ability of juvenile jack mackerel, 93–143 mm standard length, to feed on live adult brine shrimp, *Artemia salina*, was tested at the nine levels of luminance used in the tests on schooling and under the same light cycle. At 0955 hr, 55 min after a test level of luminance began, live adult brine shrimp were introduced into the tank through nozzles in the center of each tank wall. All the shrimp entered the tank in 2–3 sec and were distributed uniformly at a density of 1×10^4 per m^3. At 1000 hr fish in the group were killed and shrimp in the gut of each fish counted.

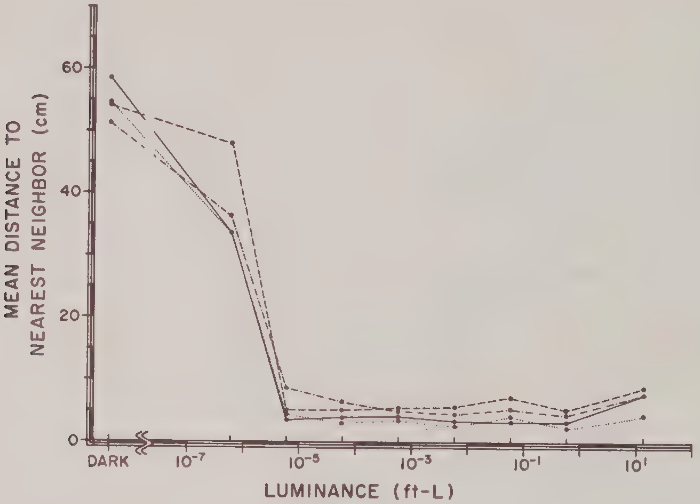

FIG. 6. Relation between luminance (logarithmic scale) and mean distances to nearest neighbor of four groups of jack mackerel at various levels of luminance. Marks above abscissa indicate positions of data points; marks below indicate logarithmic scale. Points are medians of 50 values of mean distance to nearest neighbor; lines connect the medians for each group.

Groups were placed in the tank 4 or more days before a test. They were fed daily at 0955 hr except that no food was given 48 hr before a test. One group of six fish was tested at each level of luminance except that two were tested at 6 $\times$ 10^{-6} ft-L because this level appeared to be near the threshold. Unlike the experiments on light and schooling, no photographs were taken and both the test in darkness and that at the daylight level (12.1 ft-L) were run at the same time of day as the rest of the tests, 0900–1000. The water temperature ranged from 19 to 22 C.

The techniques used to measure feeding behavior were adapted from those used on the northern anchovy by C. P. O'Connell (MS, in preparation) and are discussed in detail in his manuscript. His studies show that the number of adult *Artemia* consumed by an anchovy is linearly related to the length of the fish. Therefore, I adjusted the number of *Artemia* consumed for fish body length and expressed it as the number of *Artemia* consumed by a jack mackerel, 117 mm standard length, the mean length of the fish tested.

The first definite indication that insufficient light influenced the number of *Artemia* consumed was at 6 $\times$ 10^{-5} ft-L (Fig. 7). At one order of magnitude lower, 6 $\times$ 10^{-6} ft-L, the number consumed approached zero. Of the 12 fish tested at this level, 7 captured no shrimp, 4 consumed 3–9, and 1 fish captured 27. No fish fed in darkness. The extinction level probably was close to 6 $\times$ 10^{-7} ft-L because at this level the stomachs of three fish were empty and those of the other three contained only one or two shrimp each.

The shape of the curve for light and feeding resembled that for light and schooling but their regions of maximum slope differed. The maximum slope

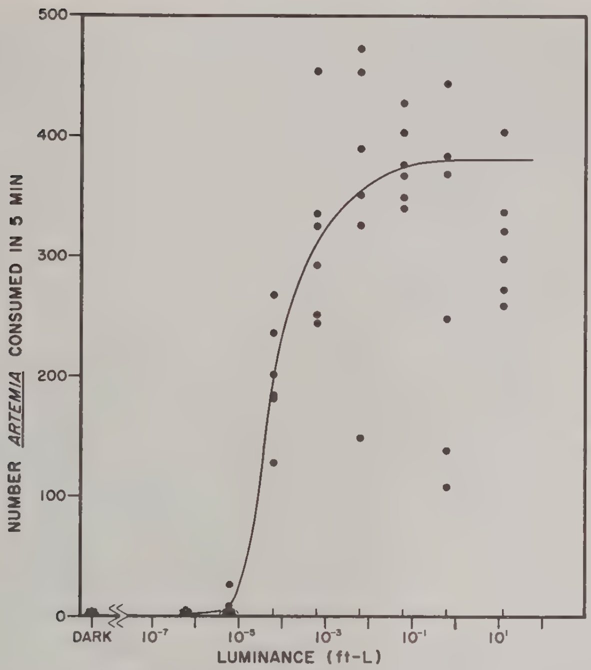

FIG. 7. Relation between luminance (logarithmic scale) and the number of adult brine shrimp, *Artemia*, consumed in 5 min by jack mackerel; each point is the number consumed by one fish after the value was adjusted for fish length. Marks above abscissa indicate positions of data points; marks below indicate logarithmic scale.

for the feeding curve was between 6 × 10^{-5} and 6 × 10^{-6} ft-L whereas that for schooling was one order of magnitude lower, between 6 × 10^{-7} and 6 × 10^{-6}. The difference in size and visibility between a brine shrimp and a jack mackerel might explain the difference in the luminance requirements for feeding and schooling.

ESTIMATES OF TRESHOLDS AND COMPARISON WITH VALUES IN THE LITERATURE

The luminance threshold for schooling was probably between 6 × 10^{-7} and 6 × 10^{-6} ft-L. If maintaining groupings for 50% of the time were used as a threshold, the schooling response at 6 × 10^{-7} ft-L would be considered to be below threshold because the medians for all indices in all groups at this luminance were only slightly different from the values obtained in the dark and the fish maintained groups of three or more fish for less than 50% of the time. Determination of the actual threshold value would require additional observations between 6 × 10^{-7} and 6 × 10^{-6} ft-L and the establishment of a threshold criterion for schooling.

The data on feeding were more difficult to interpret because they were more variable and because the response changed over a wider range of luminance. Any statement regarding a luminance threshold for feeding would have to be restricted to the density and size of prey used in the experiments. A criterion for threshold based on the presence or absence of brine shrimp in the gut would place the threshold near 6×10^{-7} ft-L. On the other hand, if 50% of the average number of brine shrimp captured in daylight, 12.1 ft-L, were used as a threshold it would fall between 6×10^{-5} and 6×10^{-6} ft-L. The latter criterion seems more reasonable because, if enough time were allowed, all fish held at 6×10^{-7} ft-L would probably have captured at least one brine shrimp.

The values of minimum illumination for schooling for other species summarized from the literature by Shaw (1961) and by Blaxter (1964) seem too high when they are compared with the values determined for jack mackerel. The value of 1×10^{-6} ft-c for minimum schooling by *Astyanax*, given by John (1964), is similar to the values for jack mackerel. John's data, however, showed a gradual decrease in schooling over a wide range of decreasing intensities whereas in jack mackerel the change in schooling occurred over a change of one order of magnitude. The change in jack mackerel might be expected if the luminance threshold for schooling is merely the minimum adaptive luminance required for fish to see other fish. Visual acuity in humans, for example, changes very rapidly as the light intensity is increased above threshold (Pirenne and Denton, 1952). The gradual decrease in schooling found by John (1964) suggests that light-dependent factors other than visual perception may also influence schooling in some species. The existence of factors other than visual perception may be indicated by the thresholds for schooling determined by Steven (1959) and Shaw (1961) because their threshold values appear to be too high to be near the absolute visual threshold.

The results of the feeding experiments agreed more closely with the values in the literature summarized by Blaxter (1964) than did the schooling data, probably because criteria for measuring feeding were basically the same (all were based on the number of prey captured within a certain period) whereas the criteria for measuring changes in schooling differed greatly. Most of the species listed by Blaxter (1964) seem to be able to capture significant numbers of prey at light intensities as low as 1×10^{-5} to 1×10^{-4} ft-c. The lower limit for effective feeding in jack mackerel, 6×10^{-5} ft-L, is of the same order of magnitude.

SCHOOLING AND FEEDING AT NIGHT IN THE SEA

I have chosen two points of reference to relate the behavior of jack mackerel observed in the laboratory to what might be expected in the sea: 6×10^{-6} ft-L as the adaptive luminance for schooling, and 6×10^{-5} ft-L as that for effective feeding. A number of assumptions must be made in order to relate fish behavior in the laboratory to their behavior in the sea. The experiments showed that jack mackerel can school at 6×10^{-6} ft-L but one must assume that the fish would show this behavior under natural conditions, and that their responses were not altered substantially by size and other characteristics of the laboratory environment.

Other problems and assumptions exist because of differences between photometric measurements made in the laboratory and measurements of light in the sea, and because of differences in spectral sensitivity between the human eye and the eyes of fishes. This problem has been discussed in detail by a number of authors (e.g. Seliger and McElroy, 1965; Westlake, 1965). Photometric measurements (foot-candles, foot-Lamberts) require that the photometric instrument receive and measure light over wave lengths corresponding to the average spectral sensitivity of a light-adapted human eye (the photometric standard observer). Most measurements in the sea, on the other hand, have been made in radiometric units (μ watts/cm^2), and the light entering the receptor is restricted to a narrow bandwidth. To convert radiometric measurements to photometric the spectral irradiance distribution at various depths for different water types must be known.

Spectral irradiance as a function of depth is available for Crater Lake (Smith and Tyler, 1967) and the Gulf of California (Tyler and Smith, 1967); the diffuse attenuation coefficients at a depth of 5–10 m are $K = 0.052$ m^{-1} for Crater Lake and 0.151 m^{-1} for the Gulf of California. The clarity of the water in the Gulf of California measurements is reasonably close to that found by Duntley (1959) in the vicinity of the Coronado Islands, an area inhabited by jack mackerel: $K = 0.18$ m^{-1}, at a depth of 3–10 m.

Richard Whitney (unpublished MS) prepared a series of graphs from the data of Tyler and Smith (1967) and Smith and Tyler (1967) in which the downwelling illuminance in foot-candles from 0 to 1200 m can be estimated from the solar radiation at the surface.

For a moonless starlit night Whitney's graphs show that a downwelling illuminance of 6×10^{-6} ft-c exists at a depth of 20 m in Crater Lake and at 10 m in the Gulf of California. On a moonless night the adaptive luminance in foot-Lamberts in the upper hemisphere of the visual field would probably be the same as the downwelling illuminance in foot-candles. On the basis of this evidence it appears that jack mackerel would be able to maintain schools near the surface on a moonless starlit night. Effective feeding on a moonless night would not appear to be possible because the downwelling illuminance just below the surface would be 1.5×10^{-5} ft-c.

When the full moon is at the zenith a downwelling illuminance of 6×10^{-5} ft-c would be present at 150 m in Crater Lake and at 50 m in the Gulf of California water (Whitney, unpublished MS). Under moonlight the adaptive luminance would not be equivalent to the downwelling illumination because the field would be brighter in the direction of the moon and darker in the opposite direction. Nevertheless, it seems likely that on a full moonlight night the adaptive luminance near the surface, at least in the brighter areas of the field, would be sufficient for effective feeding.

More visible energy may be available than the calculations indicate. Jack mackerel rhodopsin transmits maximally at 495 mμ (Munz, MS, 1957) and is closer to the maximum transparency of clear ocean water than is the photopic filter, which peaks at 555 mμ. Thus, in clear ocean water jack mackerel may be able to school at greater depths than Whitney's (unpublished MS) values indicate because they are based on the photopic curve for the average human observer. In addition, bioluminescence could increase the background brightness significantly and, thereby, improve visibility.

ACKNOWLEDGMENTS

John Taylor and John Tyler of the Visibility Laboratory, University of California, San Diego, Calif., and Frank Hester, U.S. Bureau of Commercial Fisheries, La Jolla, Calif., provided valuable advice on the measurement of light. The characteristics and design of the lighting system were based on suggestions made by John Taylor. I thank John Tyler and Ray Smith for allowing me to use their unpublished spectral irradiance data and Richard Whitney for use of his photometric conversions of their data. Kenneth John, Evelyn Shaw, and Richard Whitney read the manuscript and offered helpful suggestions. Jon Van Olst gave valuable assistance in all phases of this study.

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Fishes Beneath Flotsam

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Beneath a floating tree *moored in the open sea, a diver observes the various fishes that have gathered there. (J. R. Hunter)*

Fishes Beneath Flotsam

By John R. Hunter
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Only a few hundred yards away the water was a blue void but near a drifting tree the water was black with fishes. Birds circled above and, beneath the surface, schools of small fishes swarmed among the branches of the tree and schools of large fishes — tuna, skipjack, dolphin, and jacks — swam about the perimeter of the aggregation occasionally feeding upon the smaller fishes. What attracted these fishes to the drifting tree? How long will they stay? How long did it take for the aggregation to form? What value is it to the fishes to remain near floating debris? These are some of the questions scientists of the Bureau of Commercial Fisheries wish to answer.

Fishermen are very much aware of the attraction of drifting materials for fishes on the high seas and their value to the fisheries. American tuna fishermen routinely inspect floating materials for skipjack and other tuna. If they find a large concentration of fish they often secure a light or flag to the object and return to it daily for two to three days, each time setting the net around the fish which have accumulated there.

In 1961, American tuna fishermen caught about 180,000 yellowfin and skipjack tuna (1,400 tons) near floating debris. As many as 26,000 tuna (100 tons) have been taken near a single drifting log in only one or two days. In many parts of the world fishermen moor rafts specifically to attract fishes. These man-made objects are fabricated of local materials and their design appears to be a function of the materials; the Japanese use bamboo rafts, the Mediterranean fishermen slabs of cork, and the Indonesians palm fronds attached at intervals to a mooring line. The commercially important fishes include

not only tunas but also dolphin and many species of jacks; others have lesser or no commercial value.

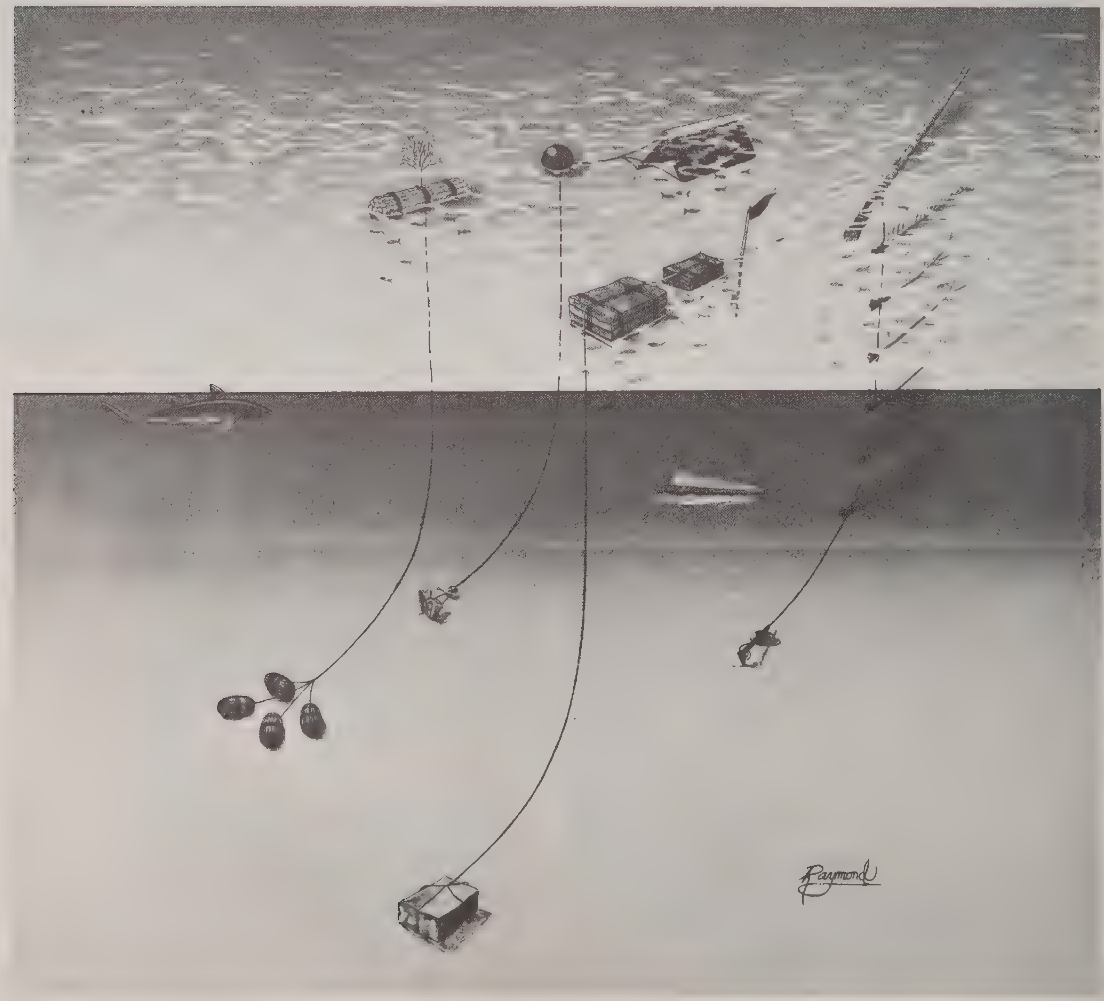
In the spring of 1963, scientists of the Bureau of Commercial Fisheries, La Jolla, California, began a study on the association of fishes with flotsam. Our goal was to provide information for the development of floating objects which would be most efficient in attracting pelagic fishes on the high seas. Our work was begun off the Pacific coast of Costa Rica, where we started by making underwater observations and collections of the fishes which had aggregated near naturally occurring floating materials.

A Cone of Fishes

Initially, when we dove beneath an object, we saw fishes densely clumped beneath it in a mass resembling a truncated cone with its top at the water surface. The fishes forming the upper part were darkly colored species and often were so close to the floating object that their fins touched it. The fishes forming the base were silvery species and often extended beyond our visual range. A few minutes after we entered the water the cone-shaped distribution, initially so striking, disappeared. The fishes left the immediate vicinity of the object and ranged outward until many of them were out of sight.

The fishes aggregated near the object in the manner described when they were disturbed by divers, the skiff, or the research vessel, and when large predators appeared. The extent to which the community aggregated in response to fright stimuli depended upon the characteristics of the stimulus; more fishes aggregated near the object in response to the initial appearance of the research vessel than to the arrival of the skiff.

The effect of different types of fright stimuli was illustrated to us one day when we were taking an inventory of the species associated with a tree we had moored. We had circled the tree with our skiff at full speed and also with the research vessel and believed that we had seen all of the associated



fishes. Suddenly many fishes appeared swimming toward the tree and within a few seconds large schools of species we had considered to be uncommon were all about us. A school of yellowfin tuna, which we had not seen, swam next to us, and fishes we were unable to photograph because they had not swum close enough were virtually pressing in against us. Then a marlin appeared, seized an adult green jack from a large school, and disappeared. More species and more individuals responded to the presence of the marlin than to any other stimulus.

Hiding in the Sea

The reaction of the fishes that led to the formation of a dense aggregation near a drifting object was the one unifying behavioral characteristic of the flotsam-associated fish fauna. All species, from damselfish one inch long to tuna, aggregated near the object in the presence of a fright stimulus. Even we humans responded similarly, swimming as close as possible to the object whenever we saw a large predator like a marlin or shark; and whenever we saw many fishes swimming toward us, we too took refuge.

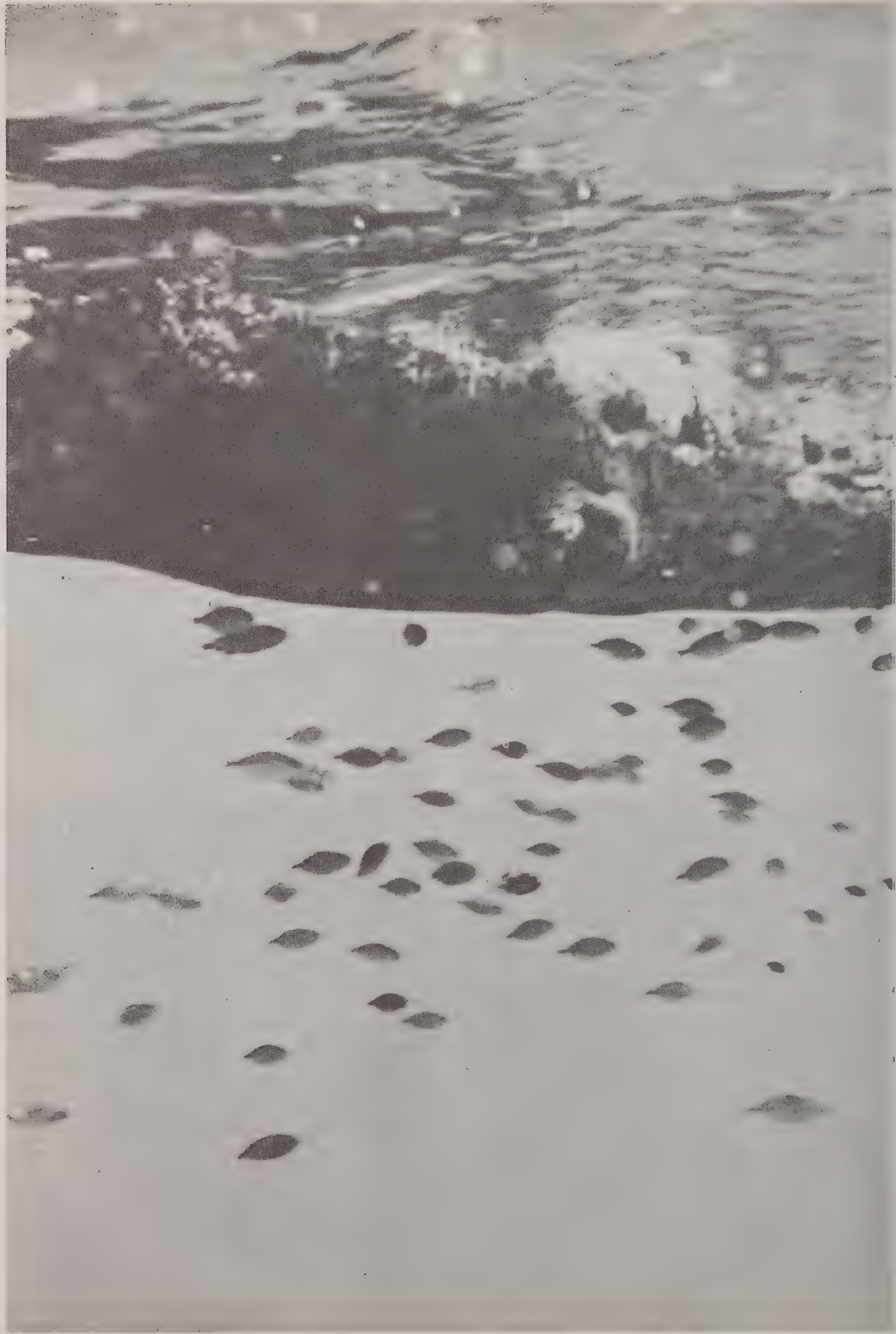
Although some fishes nearly always swam beneath or near the skiff when it drifted alongside a floating object, they remained there only temporarily. They appeared to prefer the object of their original association. On several occasions we tied a second object to one that had a population of fishes associated with it and separated the two objects 24 hours later. Invariably, the fishes remained with the original object unless we removed it from the water. If fishes were tagged and then released near their own object, they returned to it and remained there. If they were released near a strange object, they did not usually stay even though it already had a population of the same species.

Juveniles were the most common age group of fishes seen near the flotsam off Costa Rica. A few adults were often present such as those of dolphins, triggerfish, and jacks. The numbers of juvenile fishes captured near drifting materials varied from as few as ten to twenty specimens to thousands. In general we collected more juvenile fishes near large objects than near small ones. No other relationship was found between the abundance of fishes and the characteristics of the drifting materials and they did aggregate near a wide variety of objects.

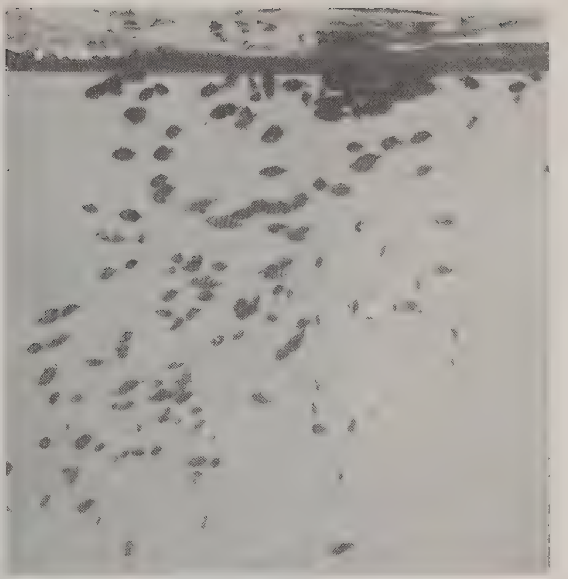
Beneath Anything that Drifts

Fishes were attracted to dead turtles or whales and to logs, branches, entire trees and even pickle bottles. Occasionally we encountered a drifting object that, in addition to numerous juveniles, also had schools of adult jacks, dolphins, triggerfish, skipjack tuna and others. These drifting objects

FLOATING OBJECTS *that have been used to attract fishes include, left to right, a bamboo raft used by Japanese fishermen, an experimental plastic object used by the author, slabs of cork used by Maltese fishermen, and palm fronds attached to a mooring line used by Indonesian fishermen. (K. S. Raymond)*



LIKE SPANGLES BENEATH A DRIFTING LOG, *left, and a wooden plank, right, juvenile fishes aggregated during the first few days these floating objects were moored. Then schools of larger fishes came. (C. T. Mitchell)*

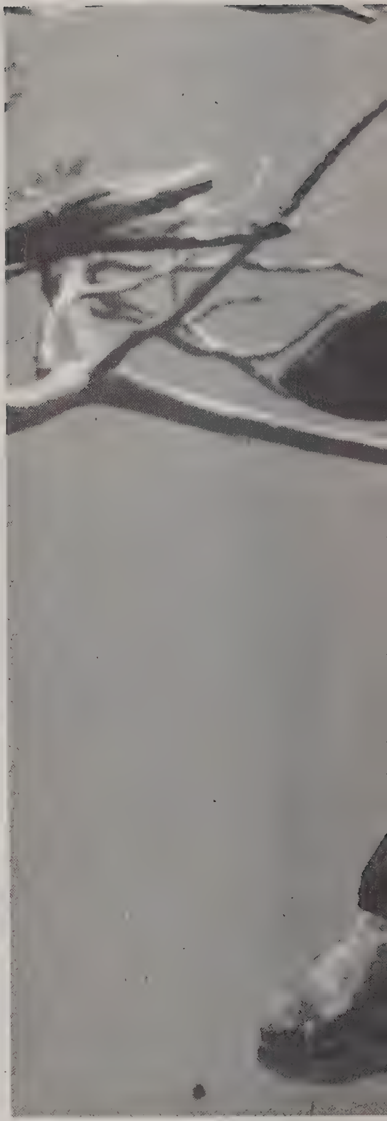


were larger on the average than those we most commonly sampled but we also found objects of large size that had attracted no adult fishes. Suspecting that the occurrence of adults might be related to the length of time the object had been at sea rather than to object size, we decided to moor objects for varying periods and record changes in species composition and abundance. Various materials such as trees, balsa rafts, and sheets of black plastic were moored about 10 nautical miles off the Costa Rican coast in about 100-150 fathoms of water.

Both Large and Small Came

Fishes began to aggregate near our floating objects within a few hours after they were moored. Five days later, hundreds to thousands of small fishes, and sometimes a few larger ones, were present. In the next fifteen to twenty days the number of small fishes remained about the same but the number of larger fishes increased. Twenty-five days after the mooring, schools of large fishes dominated the community rather than the small fishes. Schools of adult dolphin, triggerfish, black skipjack, and various jacks were common. The community continued to be dominated by the larger fishes thereafter but commonly size fluctuated with the arrival and departure of schools. I believe that the rarity of large fishes during the earlier stages of development of the community reflected their low abundance in the pelagic environment. Small fishes were more abundant and, therefore, were probably recruited in the greatest numbers throughout the time an object was present. That the population of small fishes did not increase much after the first five days may have been the result of predation by larger ones, many of which — dolphin and green jacks, for example — fed actively on the smaller juveniles. We saw schools of small juvenile threadfins just arrived at an object become

FISHES TAKE TO THE TREES. *Of the many fishes that aggregated near moored floating objects, sea chubs (with tags in dorsal fins) stayed the longest. (J. R. Hunter)*

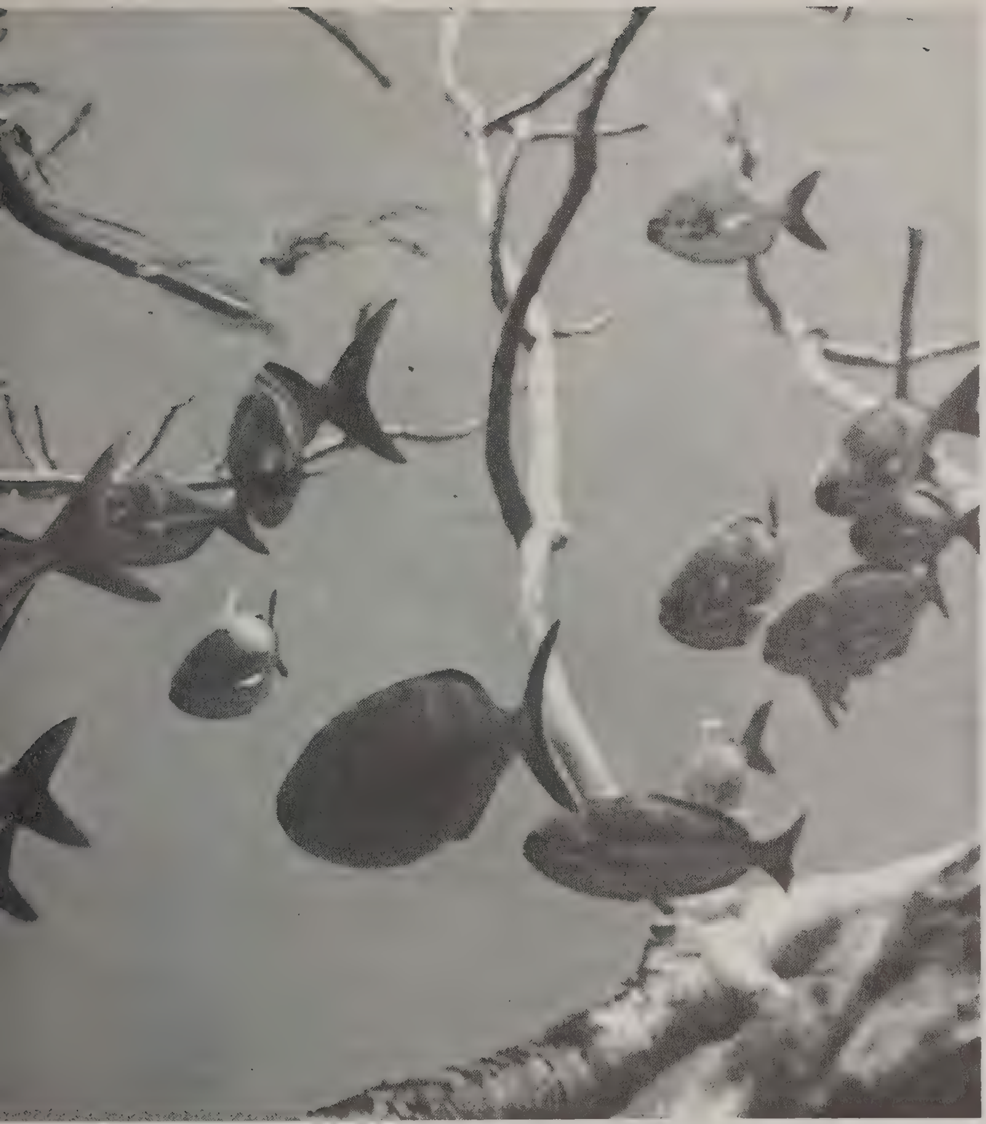


almost completely consumed by resident populations of adult green jacks.

By keeping daily records of the presence of tagged fishes and untagged individuals we were able to estimate the number of days the larger fishes remained near an object. We were surprised to find that many of the fast-swimming schooling species, such as green jacks, yellowfin tuna, and black skipjack, remained near the object for ten to twenty days. The fishes longest in residence were a group of tagged sea chubs, *Sectator ocyurus,* which were still present on the last day of the cruise, thirty-two days after they were tagged.

Why Aggregate?

The adaptive value to a species of aggregating near drifting materials is unknown. Certainly protection from predation is an obvious possibility. All species aggregated near the object when disturbed by a predator. Flotsam association is more common for juveniles, which are more susceptible to predation, than for adults, which are less so. Sometimes the protection afforded by the object is obvious. Young rockfish, for example, associate with drifting mats of kelp off the coast of California. When disturbed the rockfish enter the spaces between the fronds and branches of the mass of kelp where they are practically unavailable to predators. It is not apparent how protection is obtained for fishes at deeper positions beneath an object or those which aggregate in large numbers beneath relatively small, smooth objects. Possibly the



aggregated mass or position beneath it offers a protective advantage in a way similar to that suggested for fish schools in general (See "Schooling — Social or Survival?" *Sea Frontiers,* Vol. 13, No. 2, March-April, 1967). It is also possible that the object or the aggregation provides a fixed visual reference in a featureless environment which could be used by the fish to detect more easily the movements of predators.

Not all species which aggregate near flotsam have pelagic habits. Some that commonly live inshore probably accompany materials as they drift away from shore. Here drifting objects may aid in the dispersal of the species to other areas.

The factors responsible for the initial attraction of fishes to floating materials are also unknown. Some investigators have suggested that the large fishes come to the object because of the availability of smaller fishes for food, and the smaller ones because plankton is more visible in the shade of the object. These suggestions are not appropriate for all species because the fishes do not always remain in the shade of the object when feeding and not all of the species of larger fishes feed on the smaller ones. Adult triggerfish and filefish, for example, feed actively on salps which drift by the object. My colleagues at the Bureau of Commercial Fisheries Biological Laboratory in Hawaii have suggested that the object may function as a high-seas cleaning station where fishes come to have their parasites removed by other fishes. This view may hold for certain fishes although we have not seen parasite cleaning near flotsam off the coast of Central America. The diversity of species found near flotsam suggests the probability of many different mechanisms for aggregations.

Fishes Prefer Tents

We have just begun field experiments designed to isolate some of the factors that attract fishes to floating materials. The first experiment involved mooring variously shaped objects constructed of sheets of black plastic, generally about 5 by 5 feet, and then capturing the fishes beneath them every three days. We have tested two characteristics—vertical emplacement in the water and shape. We found that the extent to which an object hangs beneath the surface does not influence the number of fishes attracted; sheets floating flat on the water surface attracted as many fishes as those hanging vertically in the water. The greatest numbers of fishes were attracted to a plastic sheet bent at its midline so that it resembled a small tent floating with both sides submerged. We captured three times as many fishes near this object as near any of the others. Many characteristics remain to be tested: color; color pattern; brightness; and features affecting olfactory and auditory senses. I believe that this work will lead to the design of objects which may be maximally effective in aggregating commercial and sport fishes.

Fishing by Floating Devices

Floating devices might find the best commercial application in areas where schools are small and far apart because their use might reduce the searching time for schools. The attractors might be equipped with a detection system which automatically signals the size of the concentration of fishes to fishing vessels.

Floating objects might also be used as floating laboratories where pelagic species, normally difficult to observe or capture, become readily available for study. Moored instrument buoys, used to monitor ocean conditions, could be equipped with cameras to photograph at regular intervals the associated fish population and thus provide an index of the changes in abundance of pelagic fishes in relation to ocean conditions.

Field Experiments on the Attraction of Pelagic Fish to Floating Objects

By

John R. Hunter and **Charles T. Mitchell***

Bureau of Commercial Fisheries Tuna Resources Laboratory La Jolla, California

Floating objects were evaluated as fish attractants in the offshore waters of Costa Rica. Flat plastic sheets were suspended vertically in the water and floated horizontally at the water surface. Sheets that floated on the water surface attracted more fish than those suspended vertically if they had equal surface area submerged. If the outside dimensions of the objects were equal no differences existed. The most fish were attracted to a plastic sheet bent at a 60° angle at its midline so that it resembled a small tent which floated with both sides submerged.

Aggregations were dominated initially by small juvenile fishes but after about 20 days by larger juveniles and adults. Tagged fish remained near moored objects from 8 days for *Lobotes pacificus* to over 32 days for *Sectator ocyurus*. Estimates of residency were 11–13 days for untagged yellowfin tuna, *Thunnus albacares*, and 9 days for black skipjack tuna, *Euthynnus lineatus*.

The aggregation of pelagic fishes near or beneath drifting or moored objects at sea forms the basis of a number of commercial fisheries (SENTA, 1965; GOODING and MAGNUSON, in press; HUNTER and MITCHELL, 1967). Commercial quantities of fishes are captured near or beneath a variety of flotsam from dead turtles, drifting marine algae, trees and other wood debris, to man-made objects moored for the specific purpose of attracting fish. The man-made objects are fabricated from local materials and their design varies with the materials used: in Japan bamboo rafts are used; in the Mediterranean slabs of cork; and in Indonesia palm fronds attached at intervals to a mooring line. Although a wide assortment of objects attract fish, certain characteristics should make some more effective than others. If the most influential characteristics were known, attraction could be increased.

SENTA (1963) compared a bundle of straw, a sheet of vinyl, and a straw mat for their effectiveness in attracting fish but found no differences among the objects. HITOSHI IDA of the Fisheries Laboratory, Department of Agriculture, Tokyo University, is testing various types of artificial seaweeds for attraction of fishes (SENTA, personal communication). This paper explores the influence of visual characteristics of moored objects on the rate that fish gather. The objects' shape, size, and vertical displacement in the water were varied. Changes in the structure of the community of fish with time and the length of time that

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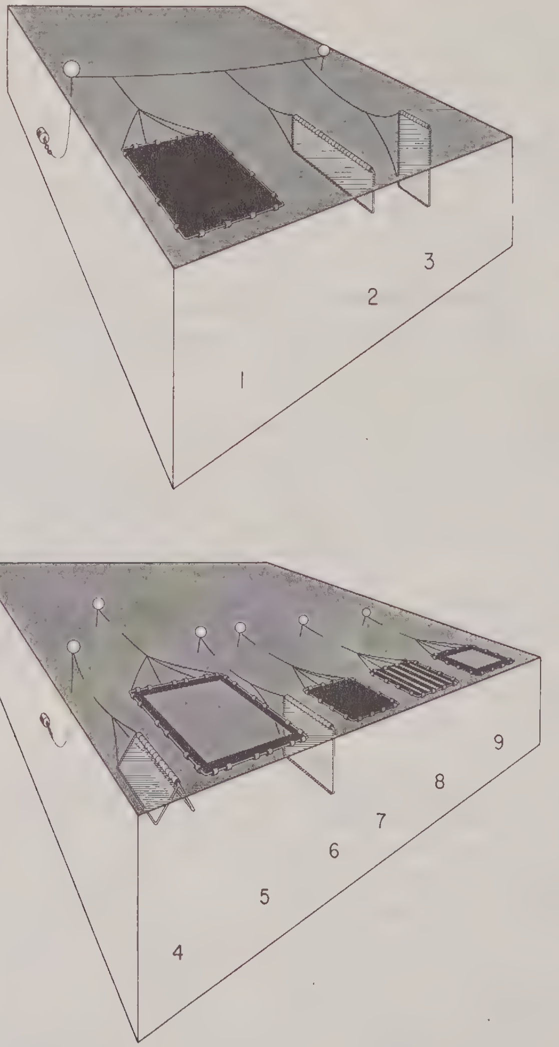

Figure 1. Upper panel, floating black plastic objects moored during 1965 in the offshore waters of Costa Rica and, lower panel, those moored during 1966. Dimensions of objects are given in Table 1.

fish resided at the moored object were also studied. The field experiments were conducted off Costa Rica at 9°45′N–85°43′W in April 1965 and at 9°45′N–85°39′W in April and May 1966. The fauna and other characteristics of the study area have been described by Hunter and Mitchell (1967).

Effect of Object Shape, Vertical Displacement, and Surface Area

The effect of vertical displacement was tested with objects that had the same submerged surface area but different vertical displacements (objects 1, 2, and 3; Figure 1; Table 1) and with objects that had the same outside dimensions but different vertical displacements (objects 6 and 7). The effect of surface area

Table 1

Characteristics of moored objects and the number and weight of the fish collected beneath each object. Objects listed by near in order of weight of catch

Object characteristics					Catch characteristics				
Object* type	Collection year	Immersed surface area (sq m)	Outside dimensions (m)	Vertical displacement (m)	Weight of fish per collection Median (g)	Weight of fish per collection Range (g)	Number of fish per collection Median	Number of fish per collection Range	Number of collection
1	1965	7·2	2·4 × 3·0	0·0	398	151–1,822	48	15– 469	6
2	–	7·2	1·2 × 3·0	1·2	108	2– 708	27	1– 269	6
3	–	7·2	1·2 × 3·0	3·0	46	0·2– 300	4	1– 230	6
4	1966	4·50	·75 × ·75 × 1·5	0·75	1,879	440–7,615	647	51–2,286	15
5	–	2·25	3·0 × 3·0	0·0	519	244–2,833	90	69– 618	4
6	–	4·50	1·5 × 1·5	1·5	481	169–5,873	233	5–1,634	10
7	–	2·25	1·5 × 1·5	0·0	481	274–2,984	204	90– 604	10
8	–	1·20	1·5 × 1·5	0·0	237	174– 646	167	32– 357	6
9	–	·97	1·5 × 1·5	0·0	222	123– 577	106	56– 205	6

* See Figure 1.

was tested in objects which floated flat on the water surface, had the same outside dimensions, but different surface areas (objects 7, 8, and 9). A three-dimensional object (4) was compared with the flat, two-dimensional objects described above.

All objects were constructed of black plastic sheets (vinyl, polyethylene, or polypropylene) attached to frames of 1·2 cm ($\frac{1}{2}$-inch) polyvinylchloride pipe. Plastic net floats of 7·6 cm diameter provided buoyancy, and lead weights were fastened to the bottom of the vertically suspended frames.

Objects 1–3 were attached at 8 m intervals to a line strung between two buoys. Objects 4–9 were moored individually; the distance between these objects was 50 m or more.

Fish which aggregated beneath the objects were collected at 3 day intervals with a miniature purse seine (Hunter, Aasted, and Mitchell, 1966). The number of individuals and weight by species were tabulated for each collection.

The species composition of the purse seine collections (Table 2) was similar to that recorded for previous years (Hunter and Mitchell, 1967). Only three species were collected that had not been taken previously; *Phtheirichthys lineatus* (43–67 mm SL), *Chloroscombrus orqueta* (36–39 mm SL), and *Uraspis secunda* (109 mm). Juvenile *Caranx caballus* dominated the collections as in previous years.

The catch-per-object was higher in 1966 than 1965 (Table 1). The lower catch in 1965 may have been the result of competition for fish among objects because of their greater proximity in that year. That the combined catch for the three objects per fishing day in 1965 was about the same as that for one of the objects of comparable type in 1966 supports this view.

More fish were taken beneath the tent-shaped object (number 4 Table 1) than beneath any of the others. The greater success of this object could be explained by a preference of fish for a three-dimensional object, that is one with surface area in both the horizontal and vertical planes. It is also possible that the tent-shape provided more protection from predation and the lower predation resulted in higher catch. The larger number of fish captured beneath the tent-shaped object can not be attributed to a tendency for them to remain

Table 2

Total weight and number of fish captured beneath moored objects in a miniature purse seine, 1965 and 1966, listed in order of weight

Species	Weight grams	Number of individuals
Caranx caballus	37,867	10,033
Decapterus sp.	12,904	2,545
Psenes pacificus	10,927	4,260
Naucrates ductor	7,071	2,919
Pseudupeneus grandisquamis	4,207	1,622
Selar crumenophthalmus	4,127	982
Canthidermis maculatus	2,744	51
Caranx hippos	2,623	990
Polydactylus opercularis	1,826	892
Polydactylus approximans	1,335	1,349
Sectator ocyurus	1,196	48
Elagatis bipinnulatus	926	336
Chromis atrilobata	462	836
*Seriola colburni**	441	4
Alutera monoceros	398	7
Uraspis secunda	109	1
Alutera scripta	54	4
Caranx marginatus	39	2
Kyphosus elegans	24	5
Balistes polylepis	17	4
Phtheirichthys lineatus	7	10
Abudefduf saxatilis	3	5
Chloroscombrus orqueta	2	2
Total	89,309	26,909

* Now considered to be a race of *S. rivoliana* (F. J. MATHER III, personal communication).

within the area between the sides. The fish usually did not remain in this area but stayed slightly below or to one side of the object.

The extent of vertical displacement of objects did not influence the catch. In 1965, fewer fish were taken beneath objects 2 and 3 which were suspended vertically, than object 1 which floated on the surface. In 1966, no differences existed between object 6 which was suspended vertically, and object 7 which floated flat on the water surface. The outside dimensions of the object rather than the submerged surface areas appeared to be the best control on size among these vertically and horizontally suspended sheets. Objects 1, 2, and 3 had the same submerged surface areas but object 1 on which only the undersurface was submerged had larger outside dimensions and attracted more fish. On the other hand, no differences existed between 6 and 7 which had the same outside dimensions but different submerged surface areas (only the undersurface of 7 submerged).

The amount of surface area was related to the catch in objects 7, 8, and 9 which floated flat on the water surface and had the same outside dimensions. Object 7 had the greatest surface area and attracted most fish. Object 9 had the least surface area and attracted the fewest fish.

Changes in the Community with Time

To study the development of fish communities over periods longer than 3 days, balsa rafts, 1·2 × 1·8 m, were moored for periods up to 51 days. Popula-

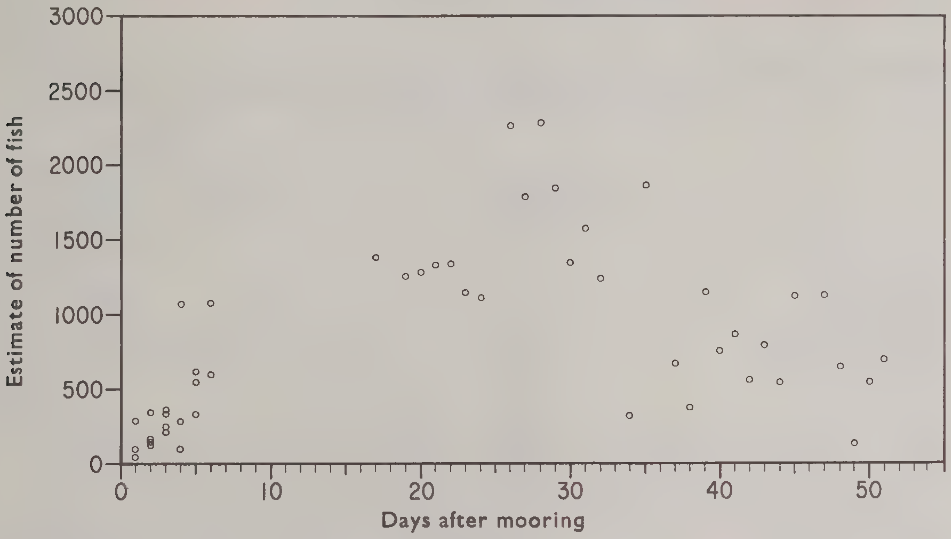

Figure 2. Estimates of the number of fish beneath moored balsa rafts. Days 1–6 are estimates taken from four rafts; and days 17–51 are from one raft. Only one estimate was made for each raft per day and no observations were made on days 7–16.

tions were not netted during the period but were estimated by divers and by automatic cameras fastened beneath the rafts. Although four rafts were moored, most of the data are from only one because the rest were lost, damaged, or stolen within 1–6 days after mooring.

Between 0900 and 1200 each day divers estimated the size and the number of individuals of each species of fish beneath each of the rafts. Automatic cameras attached to each raft took photographs at 1-minute intervals daily from 0900 to 1600. The percentage of frames exposed each day in which fish occurred was closely correlated with the daily estimates of numbers by divers ($r_s = 0{\cdot}733$, $P < 0{\cdot}001$). Because of the close agreement between these two sets of data only the estimates by divers are shown.

The number of fish increased until 28 days after mooring and gradually decreased thereafter (Figure 2). The species composition as estimated by divers changed during the 51 day mooring period. In Table 3 changes in species composition are indicated by differences in the frequency of sightings of species between the intervals, 1–6 and 17–51 days. The frequencies are expressed as a percentage of the total observations made during each of the intervals. Only one observation was made per raft per day. The size of the fish in the populations also changed during the mooring period. In days 1–6 the fish were mostly small juveniles and few large juveniles or adults were seen. After 17 days, on the other hand, the population was composed of many large juveniles and adults and relatively few small juveniles. Even in species frequently observed during the entire mooring period, *Caranx caballus* and *Decapterus* sp., the smaller individuals were more common during days 1–6 and the adults and larger juveniles during the later period.

The frequency of sightings of fish beneath the rafts during the first 6 days showed good agreement with the frequency of occurrence of species in the purse seine collections for the same year. This agreement could be expected because the purse seine collections were samples of a 3-day-old population.

Table 3

Percentage of days species were observed by divers beneath moored balsa rafts and the estimated length of the fish

	Days after mooring			
	1–6 days		17–51 days	
Species	Percentage of days with species present ($N = 19$)	Estimated length (cm)	Percentage of days with species present ($N = 30$)	Estimated length (cm)
Naucrates ductor	95	1–15	33	5–20
Caranx caballus	89	1–15	100	2–30
Decapterus sp. [1]	89	3–15	78	8–23
Psenes pacificus	84	1–8	30	8–30
Elagatis bipinnulatus	42	2–20	87	8–46
Polydactylus sp. [2]	37	2–3	7	2–3
Selar crumenophthalmus	21	5–15	64	15–30
Caranx hippos	21	2–8	0	–
Coryphaena hippurus	11	15	78	45–152
Canthidermis maculatus	5	11–25	73	11–25
Seriola sp.[3]	5	5	7	5–8
Auxis thazard	5	30	3	20
Sectator ocyurus	0	–	100	8–16
Alutera monoceros	0	–	40	20
Euthynnus lineatus	0	–	20	30–50
Thunnus albacares	0	–	20	40–70
Acanthocybium solandri	0	–	10	120
Lobotes pacificus	0	–	10	33
Uraspis secunda	0	–	10	30

[1] Specific name unknown.

[2] Either *P. approximans* or *P. opercularis* or both – specific distinctions were not possible under water.

[3] Identified as the juvenile of *S. peruana* (F. J. MATHER III, personal communication).

Residency Periods

Most of the records on periods of residency were of fish associated with the balsa life raft described in the preceding section. A few were from a balsa tree which was moored near the same locality in 1965.

Fish were captured by hook-and-line or in the small purse seine, measured, marked with small plastic tags of various colors and shapes, and returned to the raft. Daily records were kept by divers on the presence of the tagged fish.

The days of residence for the five species shown in Figure 3 are minimum values because we did not know how long a fish was present before it was tagged and because some were present at the end of the cruise. Periods of residency varied among species. Half of the tagged *Sectator ocyurus* were present on the last day of the cruise, 32 days after they were tagged. The tagged *Lobotes pacificus*, on the other hand, remained beneath the object no longer than 8 days. We were surprised to find that such a fast-swimming schooling species as *Caranx caballus* remained beneath objects for extended periods (11–19 days minimum).

Our diving notes provided information on residency periods for three species which were not tagged, *Alutera monoceros*, *Thunnus albacares* and *Euthynnus lineatus*. Owing to their size, small numbers, and the short periods which they were present, it seemed likely that we observed the same fish during these periods rather than new recruits. If this assumption is made, the following

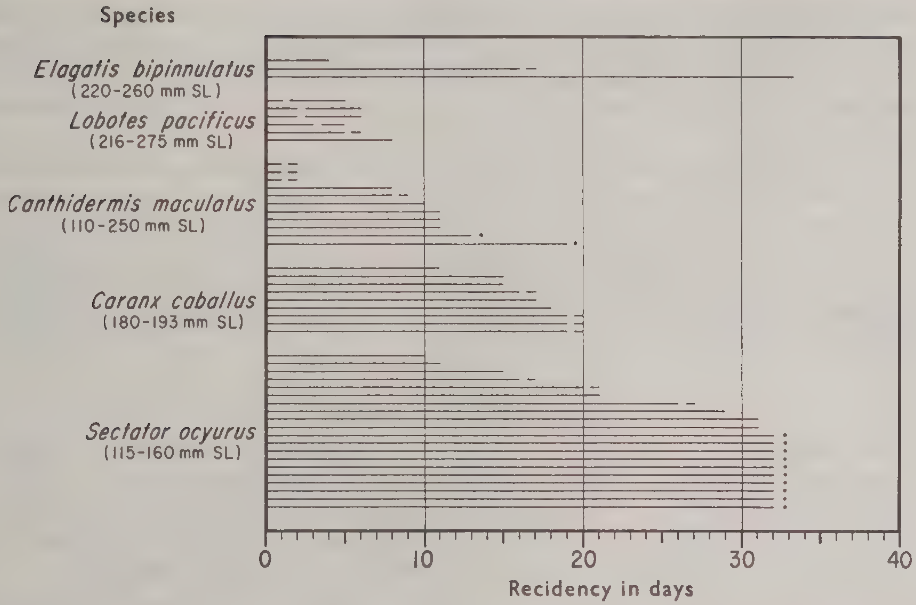

Figure 3. Periods of residency beneath a moored object for five species of tagged fish. Each black line represents the residency period for one fish. Initial segment of line represents days fish were observed; the space and second segment represents days fish may have been present but no observations were made. Dot indicates fish were present on last day of cruise.

maximum periods of residency are obtained: of eight *Alutera monoceros*, six individuals remained 8 days, one 11 days, and one 14 days; of three *Thunnus albacares*, two fish remained 11 days and one 13 days; and a school of 25 *Euthynnus lineatus* remained near the raft 9 days.

Status of Understanding of Fish Aggregations beneath Objects

The development of fish populations beneath floating materials can be described broadly from the data presented. Initially small juveniles dominate the population, and usually only a few larger juveniles and adults are present. The lack of larger fish, we believe, reflects lower abundance in the pelagic environment. Small juveniles are more abundant and, therefore, are recruited in the greatest numbers throughout the time an object is present. The structure of the population changes gradually as larger juveniles and adults accumulate near the object. Many of these fish prey on the juveniles and thereby reduce their relative abundance even though the small juveniles continue to be the dominant group recruited. By 17–28 days the population of larger fish approaches a maximum and thereafter fluctuates with the arrival and departure of individuals and schools.

This development conflicts somewhat with data and conclusions in our previous work (HUNTER and MITCHELL, 1967). We presented data in that study which suggested that little difference existed in abundance or in species composition near objects moored 5 days and objects moored 30 or more days. In the same paper we pointed out that although not evident in our purse seine data, real difference in the species composition and size of individuals appeared to exist between large and small objects. The characteristics we associated with large objects are those we now consider a later stage of population development.

In a sense we may have been correct in both cases; it is possible larger fish gather less frequently beneath smaller objects. Objects moored in the previous study were smaller than the rafts used in the present study. It is also possible that larger fish were present that we failed to see and that were not caught by the miniature purse seine. Clearly it is important to conduct a long-term mooring experiment of at least 20–30 days to evaluate the effects of differences in object size.

Acknowledgements

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Summary

Various floating objects were evaluated as fish attractants in the offshore waters of Costa Rica. The most fish were attracted to a plastic sheet bent 60° at the midline which floated with both sides submerged, fewer fish were attracted to plastic sheets which floated flat on the water surface and to flat sheets which were suspended vertically in the water. Changes in the structure of the community of fish with time and the length of time that fish resided at the objects were also studied.

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THE "MIXED LAYER" IN THE WESTERN TROPICAL ATLANTIC OCEAN[1]

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ABSTRACT

Significant differences in the thicknesses of the isothermal and isohaline layers in the so-called mixed layer are reported for the western tropical Atlantic Ocean and the eastern Caribbean Sea, on the basis of 339 coarse-scale STD (salinity-temperature-depth) records. The differences exceed 7.5 m in 45 per cent of the records and 17.5 m in 31 per cent. The significance of these dissimilarities and the possible reasons for them are discussed.

INTRODUCTION

The term "mixed layer" is customarily used to designate a layer of water immediately beneath the surface of the sea, in which the vertical gradients of conservative properties are zero. It is usually assumed that the layer was formed by wind-mixing or thermohaline convection. Common practice has been to determine the thickness of the mixed layer by measuring only one variable, temperature, thus assuming that an isothermal layer is equivalent to a mixed layer. This practice has resulted from the wide use of an *in situ* recording sensor of temperature (the mechanical bathythermograph), a lack of comparable sensors of other conservative properties, and general acceptance of a simple mixing model to explain the formation of an isothermal layer.

Vertical temperature structure in the tropical and subtropical regions of the world ocean generally includes an isothermal layer that extends from the sea surface to a depth at which a pronounced temperature gradient (thermocline) is encountered. The isothermal layer, however, is only quasi-isothermal. BT (bathythermograph) traces often show a slight vertical temperature gradient. More accurate sensors for recording temperature and depth, like those of the recently developed STD (salinity-temperature-depth) sensing systems, show that a slight variable gradient exists (Figs. 1, 2). In their study of small-scale temperature structure based on 34 STD stations in the western tropical Pacific Ocean, Stommel & Fedorov (1967) found variations of about 0.2°C from truly isothermal conditions in the layer. Notwithstanding, I refer to the layer as "isothermal" in this paper.

Vertical salinity structure in the near-surface layer of the sea is generally analogous to the temperature structure. An isohaline layer, which is found

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[1] Contribution No. 66, Bureau of Commercial Fisheries Tropical Atlantic Biological Laboratory, Miami, Florida 33149.

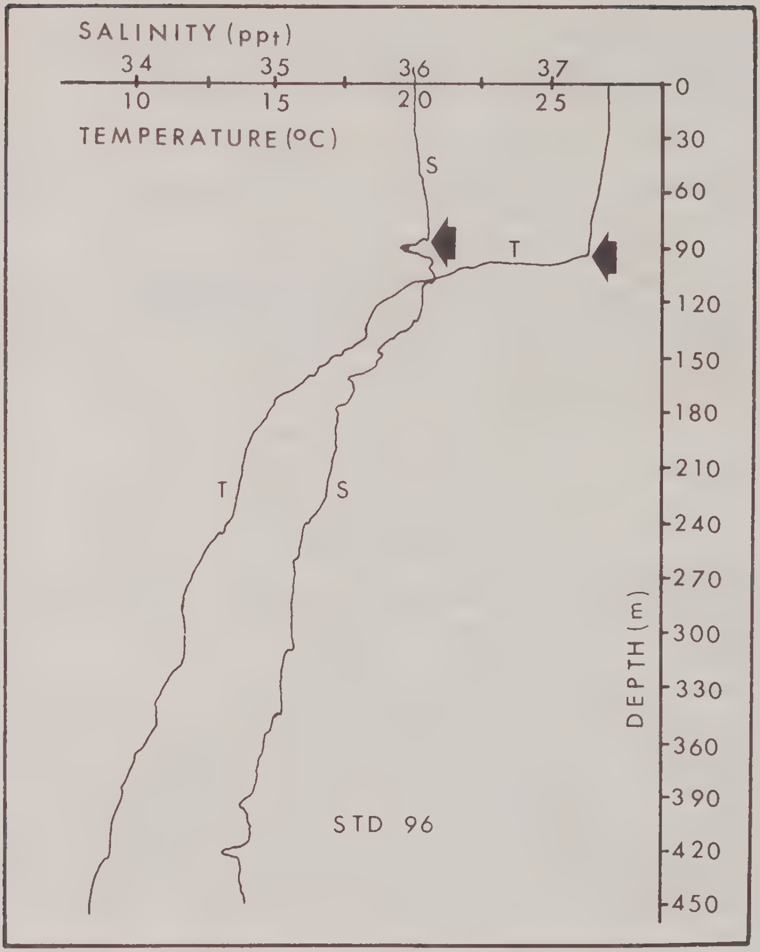

FIGURE 1. Coarse-scale record of STD lowering 96 (0°22′N, 43°43′W). Trace-line widths approximately equal to 0.1°C and 0.02‰ salinity. Salinity trace is offset in depth 7.5 m to allow the two pens to cross. Arrows indicate isolayer thicknesses.

immediately beneath the sea surface, extends down to a pronounced salinity gradient (halocline). Even though this layer is only quasi-isohaline, for convenience I here term it the isohaline layer.

Oceanographers have generally assumed that the isohaline and isothermal layers were coincident, because a continuously recording salinity sensor was not available until recently. Defant (1961) questioned the validity of the assumption when, in a discussion of the isohaline layer in the subtropical and tropical Atlantic Ocean, he stated that "its thickness is not the same as that of the thermal top layer, but is usually somewhat smaller," but he did not treat this difference quantitatively.

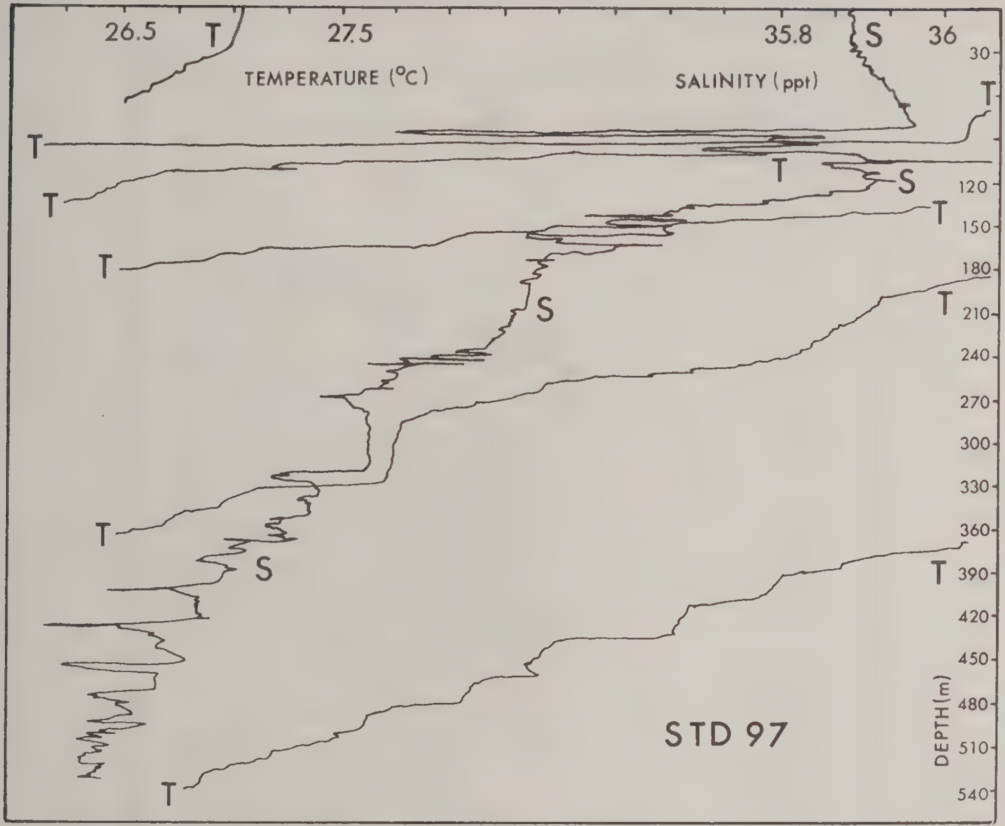

FIGURE 2. Fine-scale record of STD lowering 97 at the same position as 96 (Fig. 1). Trace-line widths approximately equal to 0.01°C and 0.003‰ salinity. Salinity trace is offset in depth 7.5 m to allow the two pens to cross.

OBSERVATIONS

STD sensing systems make possible the careful study of isothermal and isohaline layers. I studied 339 coarse-scale STD records acquired on Cruise 5 of the R/V UNDAUNTED in the western tropical Atlantic Ocean and the eastern Caribbean Sea between 18°N and 24°S. Thicknesses of the isothermal and isohaline layers were read from the records, and the difference in thickness (ΔZ) was obtained by subtraction ($Z_T - Z_S = \Delta Z$). The precision of the estimates of ΔZ is about ± 4 m. Shallow (< 7.5 m) surface layers of high temperature or low salinity were ignored in the evaluation of underlying iso-layer thicknesses.

The records yielding non-zero values for ΔZ fell into two general groups: those showing a distinct difference between thermocline and halocline depth (Fig. 3), and those showing the same clinal depths, but showing a difference in the vertical gradient of the "isothermal" and "isohaline" layers

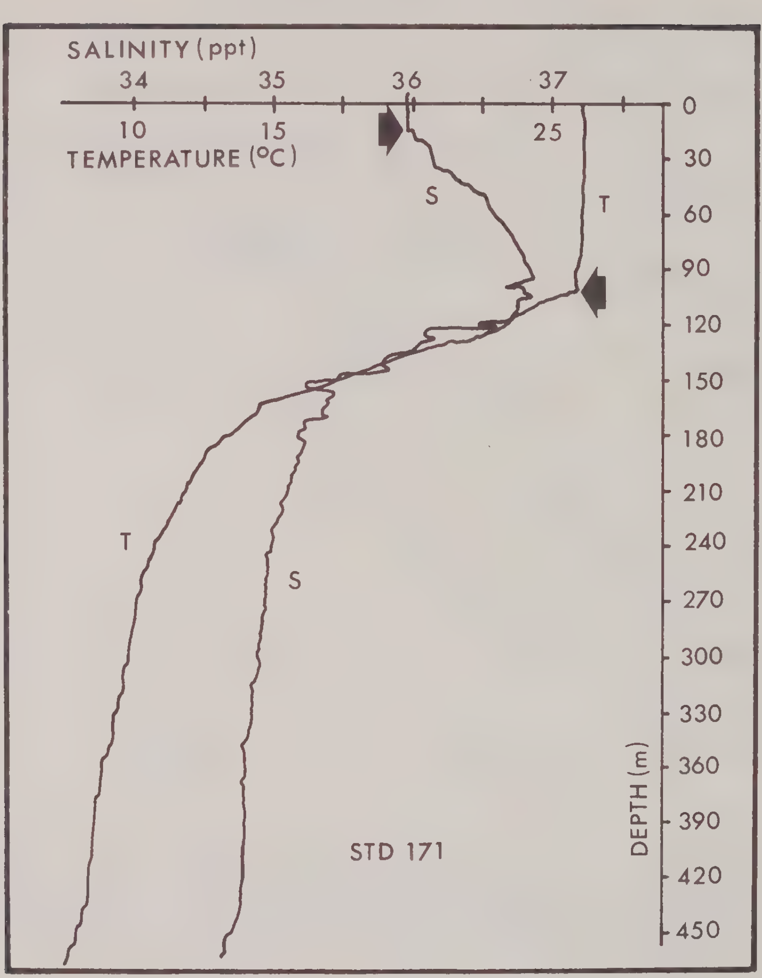

FIGURE 3. Coarse-scale record of STD lowering 171 (07°02′S, 33°03′W). Salinity trace is offset in depth 7.5 m to allow the pens to cross. Arrows indicate iso-layer thicknesses.

(Fig. 4, thermocline and halocline both at 82 m). STD records of the vertical temperature and salinity structures varied widely. To make the evaluation of the records more objective, threshold values of the vertical gradients of temperature and salinity ($\delta T/\delta Z$ and $\delta S/\delta Z$) were chosen for use as criteria in designating a layer as isothermal or isohaline. The values ($\delta T/\delta Z = 0.006$°C/m; $\delta S/\delta Z = 0.002$ ppt/m) were selected to be equal to, or greater than, the stated precision of STD temperature and salinity measurements, assuming $\delta Z = 15$ m, and to produce about the same density changes at 24°C and 35 ppt.

A histogram (Fig. 5) of the frequency distribution of ΔZ clearly shows that the isothermal and isohaline layers frequently differed in thickness:

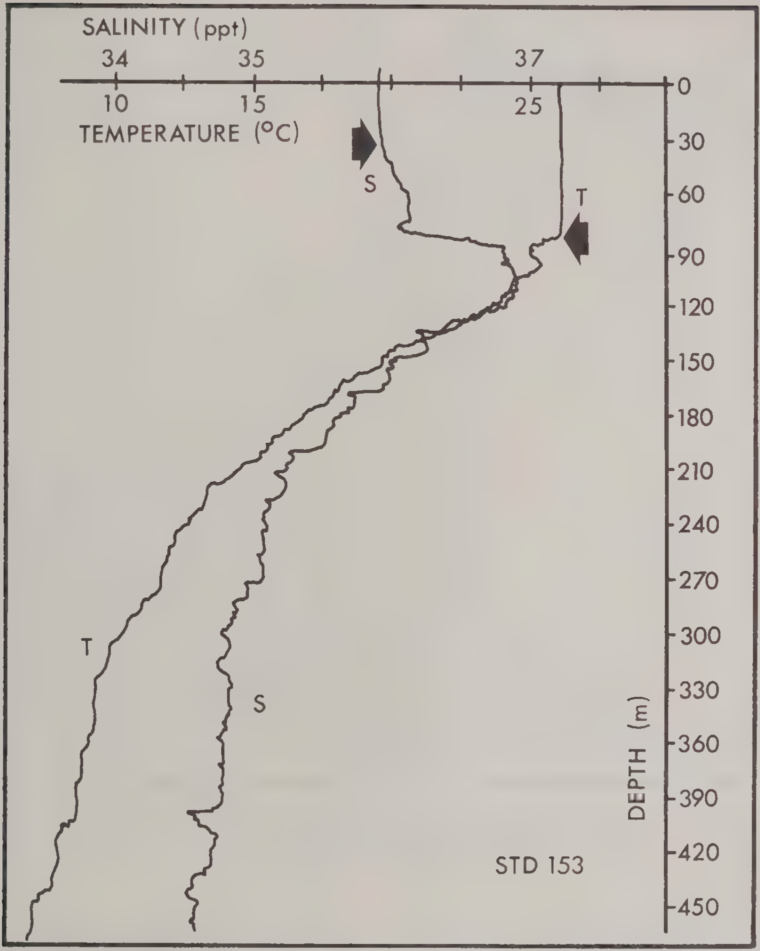

FIGURE 4. Coarse-scale record of STD lowering 153 (5°15′S, 34°37′W). Salinity trace is offset in depth 7.5 m to allow the pens to cross. Arrows indicate iso-layer thicknesses. Even though the main thermocline and halocline are at the same depth, the difference in vertical gradients above them yields different iso-layer thicknesses.

$\Delta Z > 7.5$ m in 45 per cent of the records and > 17.5 m in 31 per cent. The distribution of ΔZ is not symmetrical around the 0 class, but is skewed toward positive values with a secondary mode in the 30-m class, which is the result of a concentration of effort (52 lowerings) in a small area in the eastern Caribbean Sea.

SIGNIFICANCE OF $\Delta Z \neq 0$

Clear evidence that the isothermal layer is often not equivalent to the mixed layer in the area covered by this study casts doubt on the use of the

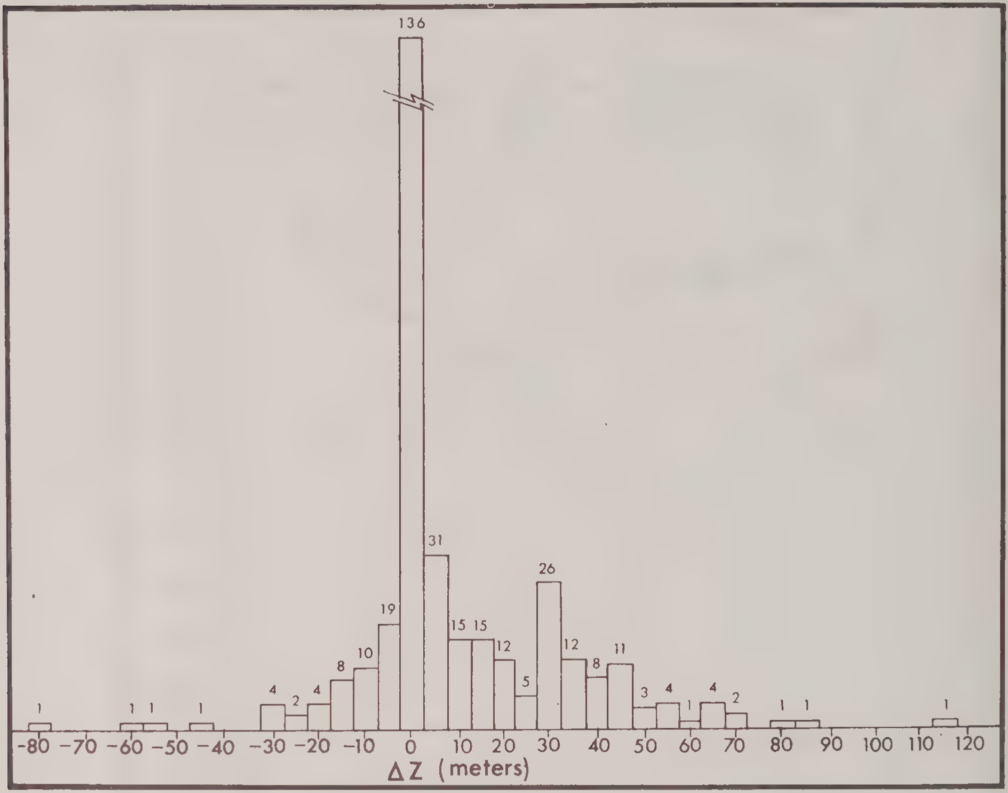

FIGURE 5. Histogram of frequency distribution of ΔZ values. Classes are centered on 5-m intervals.

thickness of the isothermal layer as (1) an aid to vertical interpolation of salinity or other variables, or (2) an indication of pycnocline depth from which to infer velocities of geostrophic currents. More important, if the iso-layers differ in thickness, it is obvious that they were not generated *in situ* by simple vertical mixing but that other processes must have been involved.

A discussion of processes that may act to form iso-layers can be found in the numerous theoretical and empirical studies of thermocline formation (reviewed by Turner & Kraus, 1967, and Tully, 1964). Simple theories, based on vertical eddy processes only, have been cited often to explain thermocline and isothermal layer formation (e.g., Defant, 1961).

The relative importance of the various processes involved in thermocline (and halocline) formation varies regionally. Tully (1964) recognized this variation and divided the North Pacific Ocean into zones according to the predominant processes. He pointed out that surface heating and cooling, freezing, evaporation, precipitation, wind-mixing, and convective mixing

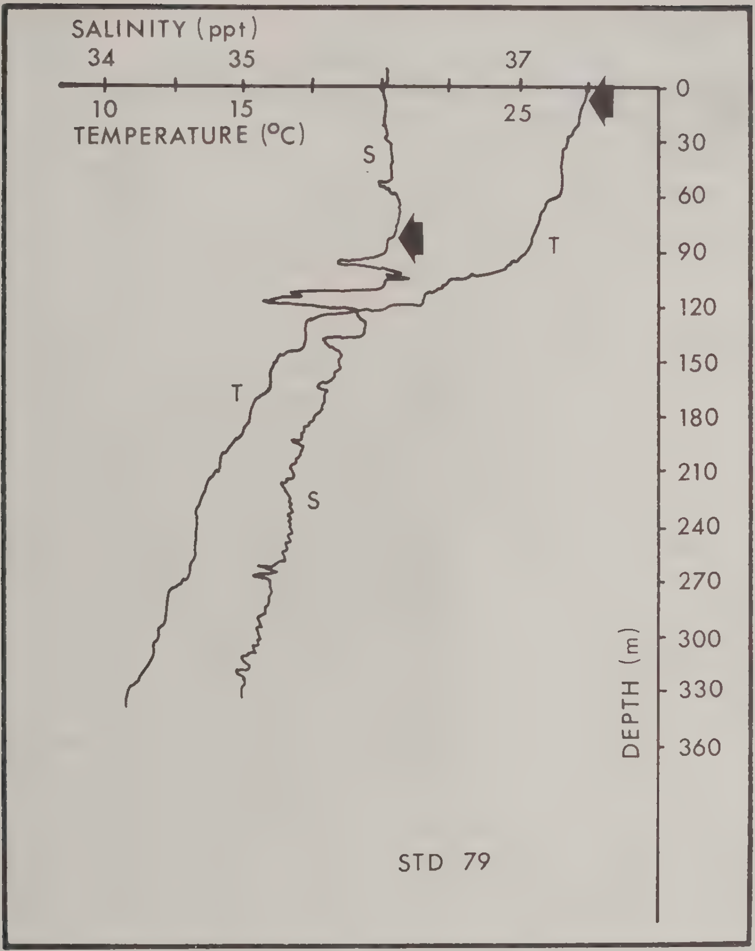

FIGURE 6. Coarse-scale record of STD lowering 79 (02°48′N, 46°46′W). Salinity trace is offset in depth 7.5 m to allow the two pens to cross. Arrows indicate iso-layer thicknesses.

determine the vertical thermal structure of sea water in regions of slow horizontal transport. In regions of rapid transport, there is too little time for these processes to produce significant changes in the water column, and its properties are advected into the region. This condition is especially evident in the vicinity of western boundary currents, which transport water of tropical characteristics to higher latitudes.

Because the data upon which the present study is based were obtained along the western edge of the tropical Atlantic Ocean in the vicinity of the Guiana and Brazil currents (two western boundary currents), advection must be considered a significant mechanism in producing the structures observed. Parts of the area under investigation also receive the effluent

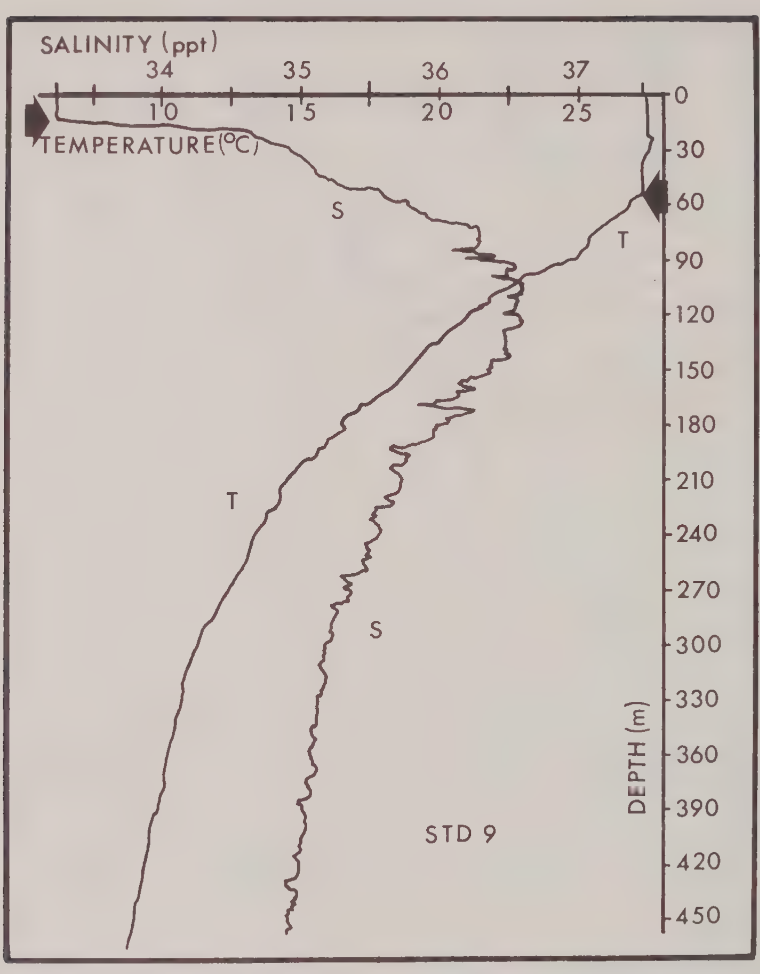

FIGURE 7. Coarse-scale record of STD lowering 9 (12°20′N, 62°31′W). Salinity trace is offset in depth 7.5 m to allow the pens to cross. Arrows indicate iso-layer thicknesses.

plumes of several large rivers, including the Amazon. The plumes enter the sea at very low salinities but at temperatures nearly matching the sea-surface temperature.

An example of a large positive ΔZ value produced by subsurface advection is found in Figure 3, which shows a strong halocline leading to a layer of maximum salinity in the same range of depth as an isothermal layer. The structure between 20 m and 105 m may have been produced by the advection of water of high salinity and temperature nearly equal to the sea-surface temperature. If the classical explanation of water-mass formation (Sverdrup, Johnson, & Fleming, 1942) applies to the formation of this layer of high salinity, then conditions must have been unusual in the formation zone—a horizontal gradient of salinity was present at the sea surface, but not a horizontal gradient of temperature.

Vertical structures of temperature and salinity yielding negative ΔZ values (isohaline layer deeper than isothermal, see Fig. 6), if similarly produced, would require the opposite condition in the formation zone—a horizontal gradient of temperature but not salinity. Claes Rooth has pointed out (personal communication) that such structures could be formed also *in situ* by wind-mixing under conditions of surface heating but negligible evaporation.

An example of a positive ΔZ value produced by advection of mixed river effluent near the sea surface appears in Figure 7; the effluent probably originated in the Orinoco or Amazon River. The upper 55 m of the water column is isothermal, but 40 m of this thickness (15-55 m depth) shows a strong salinity gradient.

Another process that could produce a difference in iso-layer thickness is the differential vertical transport of heat and salt resulting from "two-diffusivity" (Stommel & Fedorov, 1967) convection. A natural equivalent to the classical salt fountain, this convection follows an amplification of ambient turbulence arising from the hundredfold difference in molecular conduction and diffusion through the interfaces of small, vertically displaced water masses (Stommel, Arons, & Blanchard, 1956; Stern, 1960; Turner & Stommel, 1964; Walin, 1964; Turner, 1967).

Two-diffusivity convection has been observed in laboratory experiments, but never in the ocean, and its significance there is hypothetical. Such convection can occur only in regions where both temperature and salinity decrease with depth; it would therefore be instrumental in producing non-zero ΔZ values only where the salinity is greater in the surface isohaline layer than below. Effects of the convection are not clearly understood, and the resulting structure depends in part upon the duration of the convection and the pattern in time and space of the wind-mixing during the interval. Stommel & Fedorov (1967) suggested several small-scale features whose formation may involve the process, and Turner (1967) suggested that the process may cause isothermal and isohaline laminae beneath the Mediterranean outflow in the eastern North Atlantic. In the present study, I found only 25 records that indicated structures of temperature and salinity conducive to the functioning of two-diffusivity convection as an influence on iso-layer thickness. Because no consistent pattern of ΔZ values appeared in the 25 records, this study cannot describe the effects of two-diffusivity convection.

A plot of ΔZ values at station positions revealed that ΔZ varies considerably in space and time. The variability is greatest in turbulent areas, such as off the "bulge" of Brazil. Observations indicate that the water masses producing some of the ΔZ values may be non-steady state in nature and relatively small (less than 10 km in horizontal extent).

Further study similar in scope to that of Stommel & Fedorov (1967) is needed to acquire a spatial and temporal description of the masses involved and to determine the nature and significance of the mechanisms causing the observed ΔZ values. The mechanisms suggested in this paper have not been proved operative in specific cases or of general significance in the world ocean. Two principal conclusions remain valid: (1) an isothermal layer cannot be regarded as equivalent to a mixed layer; (2) the formation of iso-layers near the surface must involve processes other than vertical mixing in that part of the tropical Atlantic Ocean covered by this investigation.

SUMARIO

LA "CAPA MIXTA" EN EL ATLANTICO TROPICAL OCCIDENTAL

Un estudio de 339 reportes STP (salinidad-temperatura-profundidad) en escala gruesa, reveló una diferencia significativa en el grosor de las capas isotermas e isohialinas superficiales en una gran parte de los reportes. Las diferencias en grueso exceden 7.5 m en el 45 por ciento de los reportes y 17.5 m en el 31 por ciento. Estas diferencias son clara evidencia de que la isoterma y la capa mixta frecuentemente no son equivalentes en el Atlántico tropical occidental ni en el Caribe oriental y las disimilitudes traen dudas del valor del grueso de la capa isotermal como (1) una ayuda para la interpolación vertical de otras variables o (2) indicación de profundidad picnoclina. También, si las iso-capas son de diferente grueso, es obvio que no se formaron *in situ* por simple mezcla vertical y que otros procesos deben haber estado envueltos. Procesos tales como advección horizontal y convección de "difusividad-dos" podrían producir las diferencias observadas en la profundidad de la iso-capa.

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The Alaskan Stream south of Adak Island

W. James Ingraham, Jr.* and F. Favorite*

(*Received* 6 *March* 1968)

Abstract—Closely spaced Nansen bottle casts taken south of Adak Island confirm the presence of geostrophic velocities in excess of 60 cm/sec in the Alaskan Stream. A volume transport of 5×10^6 m^3/sec (referred to 1000 dbar) during summer increased to 10×10^6 m^3/sec during winter without an increase in velocity.

The Alaskan Stream is a boundary current which flows westward along the south side of the Aleutian Islands. Having a velocity of 40–100 cm/sec and a volume transport of about 6×10^6 m^3/sec in summer, it advects warm water moving northward along the North American coast into the western North Pacific Ocean where it has significant warming effect upon the surrounding water (Favorite, 1967). Extensive oceanographic cruises have been conducted in the vicinity of the Aleutian Islands (Dodimead, Favorite and Hirano, 1963), but because of the wide spacing of quasi-synoptic oceanographic stations (50–100 km apart), the maximum geostrophic speeds obtained have been only 30 cm/sec.

Reed and Taylor (1965), reporting on data collected in 1959, indicated good agreement between velocities of surface parachute drogues (about 75 cm/sec) and geostrophic currents (80 cm/sec referred to the 1000 dbar level) within 30 km of Atka Island. These velocities, however, were calculated from data obtained at only two oceanographic stations in the vicinity of the drogue study; although the stations were less than 10 km apart, there was an interval of 2 weeks between the observations. To determine the validity of their conclusions and to examine in greater detail the oceanographic conditions in the current system, we began a series of closely spaced observations south of Adak Island, which lies adjacent to Atka Island.

Eleven oceanographic stations were occupied in November 1965 in a line extending from the coast to over 100 km offshore (Fig. 1); nine of the stations were spaced 10 km apart (Ingraham, 1966). A similar survey was repeated in March and in September, 1966. All cruises were conducted with the R.V. *George B. Kelez*. In November the maximum depth of observation was 1000 m, but some observations in March extended below 5000 m. Neither time nor available equipment permitted direct current observations with drogues or other devices, but the information obtained indicates several interesting features of the Alaskan Stream.

Typical distributions of temperature and salinity are indicated by the data of November 1965 (Fig. 2). Relatively warm, dilute surface water flowing out of the Gulf of Alaska is forced offshore by the more saline ($> 33‰$) surface water which intrudes southward through the Aleutian passes from the Bering Sea. Although the salinity near this front is similar all the year round, the temperature gradient is usually several degrees colder inshore (due to turbulence in the passes) during summer and practically non-existent during late winter. Below 100 m, isohalines and isotherms slope sharply downward inshore, and maximum westward velocities are usually found during winter and summer shoreward of the 4°C isotherm. Observations below 1000 m obtained during March 1966 (Fig. 3), show that conditions at 1000 m were somewhat similar to those during November, and that the downward trend of the isolines extends to considerable depths. However, a level of no motion has not been ascertained in this area.

The main axis of the Stream is clearly indicated by a narrow band of high velocity flow which extends to depths of 300 m and occurred within the observed 10-km station spacing. This implies that closer station spacing should result in higher velocities. Furthermore, velocity increases as the depth of the reference level is increased. Data obtained in March 1966 show that the maximum velocity increases 1·4 times when the reference level is 2000 dbar, and 1·5 times when it is 5000 dbar.

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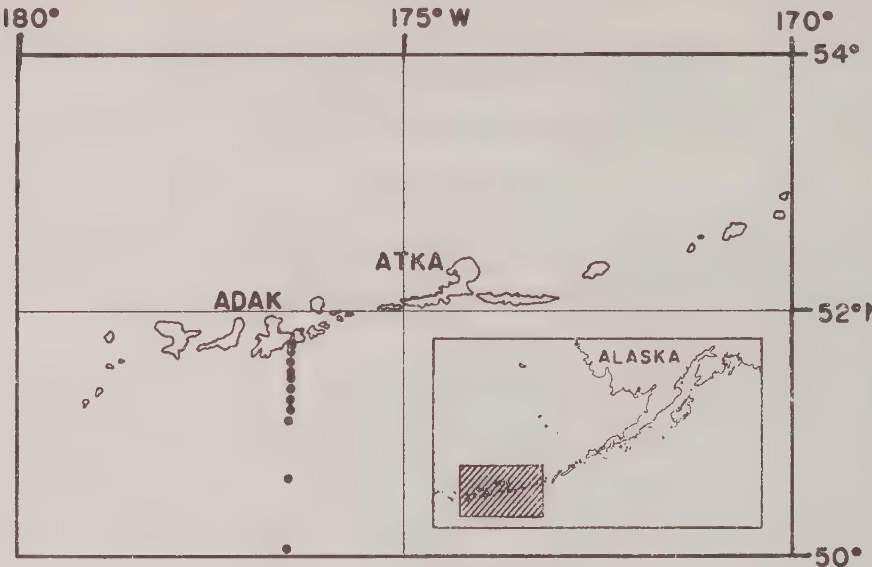

·Fig. 1. Locations of oceanographic stations south of Adak Island (R.V. *George B. Kelez*) November 7–8, 1965. A similar station pattern was used in March and September 1966.

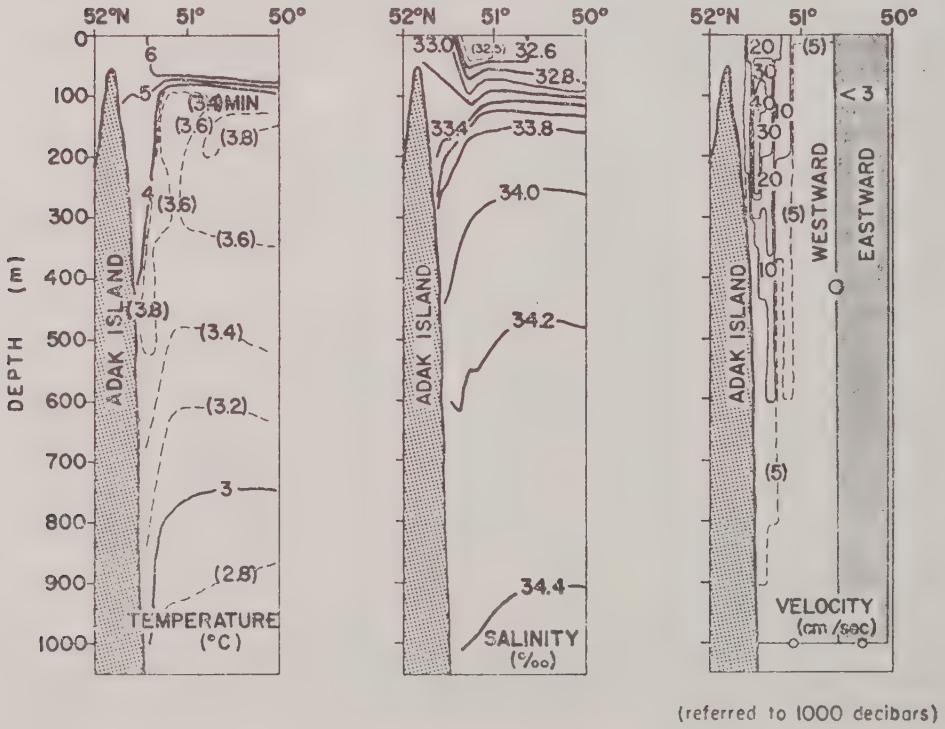

Fig. 2. Vertical sections of temperature, salinity, and geostrophic velocity (relative to 1000 dbar) south of Adak Island along 176° 25′W longitude (R.V. *George B. Kelez* (November 7–8, 1965.

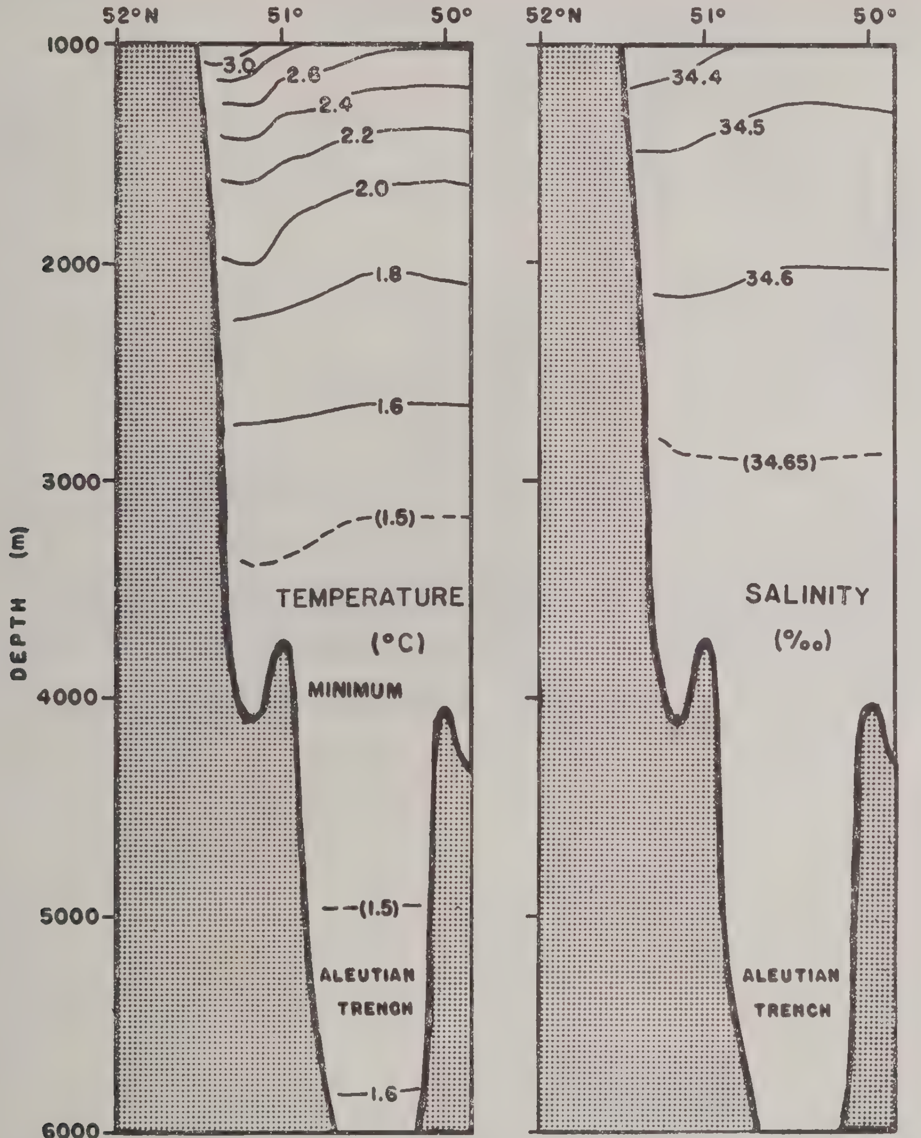

Fig. 3. Vertical sections of temperature and salinity south of Adak Island along 176° 25′W longitude (R.V. *George B. Kelez*) March 19–23, 1966.

Volume transport also increases with an increase in depth of reference level; 2·2 times using 2000 dbar and 2·5 times using 5000 dbar. The relative increases in velocity and volume transport obtained with 2000 dbar as a reference level approximate those obtained by BENNETT (1959) from data south of the Alaska Peninsula in the summer of 1955.

Comparisons of flow (referred to the 1000 decibar level) in November, March and September indicate considerable variability (Table 1). Although the width of the current, distance offshore, and volume transport were similar in November 1965 and September 1966, the depths of maximum flow and the maximum velocities were substantially different. Maximum volume transport occurred in March and was about twice that of November or September.

Table 1. *Comparison of data* (*referred to* 1000 dbar).

Date	Width of westerly surface current (km)	Distance offshore of main axis (km)	Maximum velocity (cm/sec)	Depth of maximum velocity (m)	Volume transport (10^6 m^3/sec)
Nov. 7–8, 1965	124	30	47	200	6·2
March 19–23, 1966	189	72	43	20	9·9
Sept. 9–13, 1966	115	26	61	100	5·2

Thus, geostrophic velocities in excess of 60 cm/sec and volume transports in excess of 10×10^6 m^3/sec occur in the Alaskan Stream. The westward advection of the warm, dilute surface water has a marked effect on conditions in the western North Pacific Ocean.

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ANNUAL MORTALITY OF TERRITORIAL MALE FUR SEALS AND ITS MANAGEMENT SIGNIFICANCE

by Ancel M. Johnson

ANNUAL MORTALITY OF TERRITORIAL MALE FUR SEALS AND ITS MANAGEMENT SIGNIFICANCE

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Abstract: The ages of 249 territorial male fur seals taken on St. Paul Island, Alaska, ranged from 7–17 years; the majority were aged 9–11 years. The ages of 156 males that died from natural causes were similar to the 249 killed. An annual mortality of 0.38 was estimated from the distribution of ages among these 405 adult males. An important cause of death is believed to be fighting. Few males under 10 years of age are successful in holding a breeding territory. Fifty percent of the territories on which males were killed were reoccupied within 24 hours, most replacements probably coming from the water rather than the land. Commercial use of young males could probably be increased without adversely affecting the productivity of the herd.

The primary objective of current research on fur seals (*Callorhinus ursinus*) of the Pribilof Islands, Alaska, is to determine the level at which the breeding population will yield the maximum number of salable skins. Fur seals of the eastern North Pacific Ocean spend the greater part of their lives on the high seas, returning to the Pribilof Islands of St. Paul, St. George, and Sea Lion Rock in summer to bear their young and to breed. Here, the Bureau of Commercial Fisheries of the U. S. Department of the Interior supervises the annual harvest of 2- to 5-year-old males. Females are taken only in years when recruitment of this sex exceeds the number needed to maintain the population at the desired level.

The number of males killed depends on the number of seals available on traditional hauling grounds during the period of harvesting. The degree to which a year class of males is utilized can be regulated by varying the length of the killing season, by imposing minimum and maximum limits on the size of seals taken, or by other means of varying harvest effort. The large number of mature males on the hauling grounds probably indicates that optimal use has not been achieved. Accurate estimates of the recruitment needed to maintain the population of adult males at a selected level have not been possible because the mortality was not known. Considerably more information is necessary before the optimum level for maximum production will be known. This paper presents information on the annual mortality rate of adult males as derived from the age composition of 249 territorial males killed on two areas of Northeast Point Rookery (St. Paul Island), two areas of Sivutch Rookery (Sea Lion Rock), and 156 adult males that died from natural causes on St. Paul Island beaches, in the summer of 1965. Also included is information on the rate at which animals killed were replaced.

Territorial males are physically mature animals that haul out on the fur seal rookeries of the Pribilof Islands where they vigorously defend territories from late May to early August. Pregnant females returning to the rookeries accumulate in the territories, forming harems of various sizes. Not all of the territorial males acquire harems. As a group, however, they are essentially the only males active in breeding.

The following biologists of the Marine Mammal Biological Laboratory assisted in collecting the data and determining ages: C. Fiscus, H. Kajimura, A. Roppel, and V. Scheffer.

AGE COMPOSITION

The animals used for this study were shot, and their upper canine teeth were

Table 1. Age composition of territorial male fur seals killed for study and mature males found dead, St. Paul Island, Alaska, 1965.*

	NORTHEAST POINT ROOKERY			SIVUTCH ROOKERY						
AGE	Area 1	Area 2	Total	Area 3	Area 4	Total	TOTAL BOTH ROOKERIES	REPLACEMENT MALES ON AREA 3	MALES FOUND DEAD	GRAND TOTAL
7	1	–	1	–	–	–	1	1	5	7
8	2	1	3	2	2	4	7	7	17	31
9	2	7	9	4	6	10	19	5	24	48
10	11	17	28	8	13	21	49	15	37	101
11	13	6	19	14	14	28	47	11	29	87
12	5	3	8	5	7	12	20	–	15	35
13	6	11	17	9	6	15	32	2	20	54
14	4	3	7	5	1	6	13	5	5	23
15	3	1	4	2	–	2	6	2	4	12
16	–	3	3	1	1	2	5	1	–	6
17	–	–	–	–	–	–	–	1	–	1
Total	47	52	99	50	50	100	199	50	156	405

* Replacement males were collected after they had occupied the area where the original territorial males were killed.

processed to reveal annual growth layers, by the method described by Scheffer (1950*a*:310), as modified by Wilke et al. (1958). The age of each seal was determined by three people.

The age composition of 199 territorial males collected from the two rookeries and 156 males found dead was similar (Table 1), as indicated in a Chi-square test by the high value of $P (0.3 < P < 0.5)$.

The age composition of 50 males that had replaced 50 territorial males killed on one area was similar to that of all territorial males killed; the number of replacement males killed was too small, however, to permit a meaningful test for difference.

In all samples of territorial males, ages ranged from 7–17 years; 70 percent of the animals were aged 10–13; the modal age was 10 years. Males apparently are not highly successful in obtaining territories before age 10, and few remain or are successful in holding a territory on the rookery by age 15 and older.

Osgood et al. (1915:20) reported that a male seal is capable of breeding at age 4 or 5 but normally does not breed until the 6th or 7th year, and that length of life is 12–14 years. These conclusions were apparently based on observations of marked males of known age actively defending territories, but quantitative data were not presented. In a study of the development of testes and bacula, Scheffer (1950*b*:388) deduced that "the male fur seal reaches prime condition in about the tenth year. It is likely that he is both physically and sociologically prime as a ten-year-old." The data from the present study agree with Scheffer's conclusion.

ANNUAL MORTALITY

The rate at which territorial males are replaced can be estimated from the decrease in abundance of males with an increase in age. This estimate presumably represents annual mortality, but may not, as it is possible that a male may lose his territory but may not die. The estimate was obtained by using the equation (modified) of Chapman and Robson (1960:354):

$$\hat{a} = 1 - \bar{x}/(1 + \bar{x} - 1/n),$$

where

$\hat{a}$ = estimated annual mortality,

n = number of animals in the sample,

and

$\bar{x}$ = mean age with ages coded beginning with age of full recruitment as zero.

If age 10, the most abundant age group among the samples, is used as the age of full recruitment, the estimated annual mortality based on all males 10 years old and older is 0.38. The 95-percent confidence limits are 0.35 and 0.41.

The following assumptions must be true if the above method of calculating mortality is to give valid results: (1) survival is constant for all ages beyond the age of full recruitment; (2) the distribution of ages in the sample represents that in the population; (3) the number of males > 9 years in the population is constant; and (4) recruitment of males > 9 years is constant. For a more comprehensive discussion of the assumptions and methods, see Ricker (1958) and Chapman and Robson (1960). Assumptions (1) and (2) are believed applicable to studies of fur-seal mortality, but assumption (3) is obviously not valid because according to counts, the numbers of territorial males have decreased about 20 percent since 1962. Recruitment to the population of males—assumption (4)—apparently is not constant either. The number of 13-year-old males in the sample was relatively large. Extreme fluctuations (range: 19,000–80,000) in the total number of males taken from most year classes since 1952 indicate that the survival of young males has varied considerably. The kills from year classes 1952, 1956, and 1958 deviated considerably from an average of about 59,000 males taken from year classes 1950 through 1960. Year classes 1952 and 1958 each yielded a kill in excess of 80,000, whereas only 19,000 males were taken from the 1956 year class. The 1958 year class, though large, contributed very few animals to the samples of adult males. Though it is unlikely that fluctuations in recruitment are of the same magnitude as variations in kills from the year classes, the variations in kills strongly suggest that some fluctuations in recruitment do occur.

By substituting for the assumptions of constant recruitment and survival, the assumption that recruitment and survival are random fluctations about some mean values, the estimate of mortality can be calculated from regression of the logarithm of the number in each age on age (Chapman and Robson 1960:355–356). The estimate of annual mortality based on this method is 0.37 (95-percent confidence limits, 0.29 and 0.41).

If variations in recruitment caused a 20-percent decline in the number of mature males since 1962, the estimate of mortality (0.38) based on the distribution of ages in the sample is too low. Assuming that low kills mean low escapement and hence low recruitment, the kill from each year class can be incorporated into a weighting factor. This procedure did not improve the distribution of ages. Another, but less likely, possibility is that the kill from a year class may be negatively related to escapement and low kills result in high recruitment. This approach produced an even less likely distribution of ages.

The annual counts of mature males on the Pribilof Islands show that this segment of the population changed very little from the early 1950's until 1963. Therefore, it is probably safe to assume that recruitment through 1962 was constant and calculate a mortality rate based on ages unaffected by the decline in recruitment after 1962, that is, ages $\geqslant 13$. The resulting estimate of mortality is relatively high, 0.54, for ages 13 and older. A similar estimate of 0.59 for males age 10 through 12 was calculated under the assumption that recruitment was constant for these ages.

Errors in determining ages could also bias estimates of mortality based on age composition. Though a recent analysis of errors in determining the ages of females (Marine Mammal Biological Laboratory 1967) suggests a tendency to "under-age" the canine teeth of fur seals, I do not believe that errors in determining the ages of males used in this study were biased to the extent that they would substantially increase the estimate of mortality. "Underaging" these males would affect estimates of mortality only if assigned ages were consistently less than actual ages and increasingly so with an increase in age. Even so, the method of estimating mortality described by Heincke (1913 in Ricker 1958: 42; 2.4) would decrease the effect of errors in determining age. The estimate of mortality by this method was 0.32.

Because no good basis exists for correcting the estimate based on all males ⩾ 10, the value 0.38 is presented as the best estimate of annual mortality of territorial males. This rate agrees with an estimate of annual mortality of 0.36 calculated by Chapman (1964:659) from the age composition of 110 males 7 years old and older in pelagic research collections. Peterson (1965) concluded from observations of 18 tagged and marked territorial males that annual mortality was 0.33.

IMMEDIATE REPLACEMENT OF TERRITORIAL MALES

On Northeast Point Rookery where 100 territorial males were killed June 18–25, 1965, several counts of adult males moving into the two areas were made to determine how quickly territories were reoccupied. Only occasional counts were made on the two areas on Sea Lion Rock where territorial males were killed.

Within 24 hours, 50 percent of the original number of territorial males had been replaced (Table 2). Occasionally, a male tried to occupy a territory within 2 or 3 minutes after the original holder had been killed and before the data had been collected from the dead animal. When 35 males killed on Northeast Point Rookery were removed between 9:00 AM and noon, 13 males had moved into this area by noon, and this number had increased to 17 by 4:00 PM. Fifty-two males were killed during the entire day and by 8:00 PM, 26 males had become established.

Table 2. Rate of reestablishment of territories in areas where territorial male fur seals were killed.

DAYS AFTER ORIGINAL TERRITORIAL MALES WERE KILLED	ORIGINAL NUMBER OF TERRITORIES*	TERRITORIES REESTABLISHED	
		No.	%
0	100	33	33
1	127	74	58
2	100	72	72
3	75	55	73
4	150	129	86
5	112	89	80
6	100	95	95
8	36	32	89
10	102	103	100
12	36	35	97
19	52	56	100

* Not all areas were observed every day.

Males with territories overlapping the boundaries of the study areas may or may not have been included in counts of replacements, depending on where they were located in their territory during the counts. This source of error accounts for some of the variability in counts of the number of males moving into the area. The areas appeared completely reoccupied, however, by about the 6th day after the original territorial males were killed. Beginning at the water's edge, replacement males established territories progressively farther inland.

Males established on a small section of rookery adjacent to an area where territorial males were killed were counted periodically to determine if they would forsake their territories in favor of the area formerly occupied by other adult males. On June 20, 22 territorial males were on this section. On June 21, nearby territorial males were killed. Succeeding counts were: 24 males on June 24; 19 on June 25; 32 on June 27; and 37 on July 3. Because the number of territorial males counted on the adjacent section increased rather than declined, I assumed that none had moved into the study area during the 13 days.

Nonterritorial males are scattered along the fringes of the rookeries and others are consistently observed "patrolling" the rookeries just offshore, seemingly awaiting their chance to haul out and establish territories. That this is their intent became clear when several came from the water and established territories while data were still being collected from the males killed. On the basis of these observations and the counts of territorial males adjacent to the study area, I conclude that nonterritorial males replaced established males killed for this study.

CONCLUSIONS

Few males less than 10 years old are capable of obtaining and holding territories on the rookeries. Age and body-measurement data collected during this study (Marine Mammal Biological Laboratory 1967) and obtained from other sources (Scheffer and Wilke 1953, North Pacific Fur Seal Commission 1964) show that the male fur seal is not fully grown until age 8 to 10 years. At the present level of the territorial male population, competition for a place on the rookery during the active breeding season is apparently so intense that a male that is not full-grown has little chance of obtaining and holding a territory.

The similarity in the distribution of ages among males found dead and among territorial males killed for study, and the agreement between the estimate of mortality from this study and that by Chapman (1964) for adult males collected pelagically, indicate that the estimates can be applied to the entire adult male population, territorial and nonterritorial.

The annual mortality (0.11) of adult females calculated by Chapman (1964:661) is less than one-third that of adult males. Apparently the competition for territories, and other rigors associated with the breeding season, increase the mortality of adult males. Many of the males found dead had wounds from fighting so it is likely that the competition among males to obtain and hold breeding territories is an important cause of natural mortality.

The brief span of time between the killing of males and reoccupation of their territories by other adult males would indicate that many adult males do not have territories and that in spite of a high mortality rate, there are numerous excess males. These excess males probably increase the competition for a territory on the rookery and thereby increase mortality. The number of adult males necessary for maximum sustainable yield is not known, but it appears that young males can be utilized at a greater rate without having an adverse effect on production of young. When a level has been selected at which to keep the territorial male population, it will be possible to adjust utilization so that the escapement of young males will be just sufficient to provide the necessary recruitment and keep utilization maximum.

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FOOD AND DRUGS FROM THE SEA: SLEEPING GIANT OR DECEPTIVE ILLUSION

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SLEEPING GIANT OR DECEPTIVE ILLUSION

By

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DR. JONES

The sea has been known to man and been a challenge to him for all recorded history. Harvesting the sea for food has been an important part of this challenge.

From the beginning of his history, man has exploited the oceans for food, as evidenced by the coastal migration routes of early peoples (these routes assured a readily available supply of food) and the transport and trading of marine products (fish bones have been found in inland caves of the Late Old Stone Age culture).

A study of ethnic marine biology from early written records shows that during the Egyptian civilization certain fishes were known to be poisonous, and as early as 600 A. D. the Chinese used the products of these fishes as drugs to treat certain maladies.

Later when man changed to an agricultural existence, fishing and farming advanced at comparable rates. In Europe the great herring fisheries in the eastern Atlantic developed at about the same time as the rapid increase in agricultural production in central Europe. In colonial North America fishing in offshore waters rivaled agricultural development on the frontier. The whaling industry, for example, grew rapidly in New England, and in 1846 the 746 American whaling ships far outnumbered foreign vessels in the world fleet.

In more recent times agriculture in North America has outdistanced the fishing industry. With an abundance of land to be brought into production, less consideration was given to the sea as a source of food.

The industrial revolution and its resulting technology was applied to the land but did not affect the less penetrable ocean environment. In many countries this gap between fishing and agriculture did not become so large. In Japan, for instance, because of a long history of dependence on the sea—the Japanese population pressure has required that the sea furnish up to 80 per cent of the meat protein. In other cases—for examples, the U.S.S.R. and Peru—the gap was wide until recently but has been narrowed in the last decade by the development of entirely new national marine industries.

Of the world's 200 million square miles, about 70 per cent is ocean. As we have already seen in this conference, this area of our planet holds relatively unexploited natural resources. Today we will consider a segment of these—the living resources of the sea. What are our requirements for these resources? Do we have the technologcial know-how and the economic incentive to exploit them?

The Requirement

Without doubt the food industry today is on the brink of great expansion. The situation is this: human populations are growing tremendously; in some regions they have far outstripped their food supply. Stavation is widespread throughout the world. No country is quite free from it, not even the United States, and in some countries it is a chronic public ill.

World population is expected to increase from 3.3 billion in 1965 to 5.0 billion in 1985 and to range between 6.0 and 7.5 billion by the year 2000. This is an increase of about 1.75 per cent per year. At least 20 per cent of the 2.25 billion people living in developing countries receive too few calories and the diets of about 60 per cent are inadequate in nutritional quality.

At the present rate of population increase, by 2000 A. D. there will be more than four times as many people in the developing countries as in the developed ones. We know that food requirements in developing countries will at least double in the next two decades. This represents a staggering food problem which needs to be coped with now—not 5 or 10 years from now.

The world desperately needs protein and at a cheap price to meet the food requirements of the developing countries. This is a tremendous challenge. The magnitude of the feeding task facing mankind is easily underestimated.

If present-day China were to improve its nutritional standards enough to enjoy the Japanese diet, this requirement alone would necessitate a doubling of the world fish catch. The outstanding fact is that fish—more than meat or milk—constitutes the animal protein source of a wide proportion of the world's total population. On a worldwide basis, the demand for food fish is expected to rise 3 or 4 per cent per year in the next 10 years. If fish meal and similar products are added, the total increase will be 4 to 5.5 per cent per year.

The world food problem has troubled political scientists and economists for a long time, but never before has it been the subject of such a "political movement" as is now underway. We have committed ourselves, with missionary zeal, to fight hunger on a worldwide basis.

The problem has been approached by numerous councils and commissions of the United Nations and the developed countries so that any conference on this subject has for background material scores of reports probing problems to do with future food needs and demography. The President's Science Advisory Committee on the World Food Problem says "It is imperative for programs designed to alleviate protein deficiency to produce big results in a relatively short time. Since even the most vigorous efforts probably will fall short of the goal, work should be initiated promptly." Our government is committed to a massive effort by the United States and other nations to help the less fortunate of the earth to help themselves.

Hunger is not a major problem in most parts of the United States. The problem is: Can foods of marine origin compete successfully with non-marine proteins for a place in the national diet? The per-capita consumption of food fish has remained steady for a number of years but that of non-food fish has increased. As our population has grown, this has meant a continually expanding market for fishery products, but domestic production has not kept pace with the demand. The shortfall of domestic production since 1937 has forced the United States to become the major buyer of fishery products in the world market.

Looking toward the future, we estimate that the U. S. population will exceed 230 million by 1975. Merely to maintain the present per-capita consumption of fish would require an additional catch of 1.7 billion pounds of fish and shellfish by 1975. Sixty-seven million pounds of shrimp will be required over the present 210 million pounds per year.

The Resource

Accepting the premise that we are faced with a staggering food deficit in the years ahead, we next ask the question (1) Can the oceans contribute significantly to meeting this food deficit? and (2) Are there sources of protein, other than those from the ocean, that can be harvester efficiently?

The ocean does hold vast untapped resources. The exact extent of these resources has been the subject of much speculation, but this is largely an academic question. Even the most conservative estimates quote yields several times the present harvest. The present world catch of 55-million metric tons could as a minimum be increased to 200-million metric tons according to most fishery experts.

The rapid growth of the world's marine fisheries in the last century also offers proof of the potential of these resources. No other food commodity has shown an increase comparable to that of fish. In the last century the total fish and shellfish catch increased from a couple of million tons up to the present figure of 55 million tons. According to Food and Agricultural Organization statistics (1935-60) fish has lead in expanded production among all foods, exceeded only by citrus fruits and sugar. This expansion gives indication of the latent potential present in the world's fisheries and also the economic and social pressures that have led to expansion in this field.

World Aquatic Harvest

Year	Million Metric Tons
1850	2.0
1900	4.0
1920	9.5
1938	20.5
1948	19.5
1958	32.1
1960	37.8
1966	55.0

United States fisheries in the past have been characterized as fishing selectively for particular species and the effort has been concentrated on only a handful of species. In fact, off our coasts some of the richest waters in the world contain vast unexploited and under-utilized resources. I share the view of the Department of the Interior that the time has come to utilize these resources. If we do not, other nations will find it profitable to do so.

The potential for increasing harvests is good. An estimate of the sustainable yield of the resources in areas traditionally fished by American fishermen indicates that these resources are capable of producing at least 5 or 6 times the present yield—or about 14 million tons per year. It is clear that the present limitation on the harvest from the sea is not the size of the resource, but rather a question of economics.

It is, of course, more difficult to answer the second question, "are there sources of protein, other than from the ocean, which can be harvested efficiently?" A crystal ball would have been handy to have several times during this conference, but I believe that we can make an educated guess.

The food requirements of the world are so large and also so diverse—in terms of needs and dietary habits—that more than a single solution to the problem will be required. Agriculture, food from the oceans, oil protein concentrate, and single-cell protein sources are all important. To consider one of these and at the same time exclude the others is unrealistic; all solutions require our attention.

Probably most of the available solutions will play an important part in meeting world food needs in the next 20 or 30 years. Our intention today is to convince you that the United States possesses both the reason and the resources to expand its production of food and drugs from the sea. I wish to challenge the speakers who follow to assess our industrial capability for meeting these needs.

The Capability

One of the most spectacular postwar happenings on the global food front was the emergence of the USSR and Japan as major worldwide fishing powers. Why these countries, rather than the U. S.? In terms of geographical location and industrial technology, this was an unexpected development.

How did Russia, the land giant of the world, manage to move to the sea to supply her millions with proteins? This is in many ways a more revolutionary feat than the resurgence after the war of Japanese fisheries. Japan, having lost her fishing fleet during the war, re-emerged as a dominant factor in world fisheries and regained her former status as one of the world's leading fishing nations. It was not anticipated, however, that this would happen on a global scale and that almost the entire world ocean was destined to become Japanese fishing grounds.

Japan and the USSR today appear predominant in the large-scale exploitation of the oceans. Nothing has been left to chance; their success is the result of major, daring, and progressive plans, based on sound technology and thorough financial planning.

While Japan and the USSR expanded their high seas fishing fleets after 1945, the United States took no aggressive leadership in the area. Nevertheless, left solely to private industry, segments of the fleet did expand—notably the high seas tuna and shrimp fleet. Today American boats in these fisheries are competing successfully with foreign vessels in these worldwide fisheries. The Bureau of Commercial Fisheries, under the Interior Department, is providing aid.

American shrimp vessels and American-owned companies operate in Central and South American countries and in other parts of the world. American-owned tuna vessels fish from Lower California to Peru, and in the Atlantic off Brazil and West Africa. These fleets are leaders in these world fisheries. Recently three tuna purse seiners returned to Puerto Rico from a 2-month fishing trip in the tropical Atlantic Ocean with a half-million dollars worth of fish.

The United States needs to reach the basic understanding that food is the key to world diplomacy and take the lead in this development to the benefit of the world. In the United States, we boast of the power of our competitive economy, our managerial and governing skills, our scientific and technological contribution to human progress, our elevated standard of living, and the high level of education and training of all of our people—which give us industrial strength and good government. It is time that we lived up to these claims; the exploitation of the oceans for food is a challenge to do so.

The market for fishery products in the United States has increased and market demand is good: population has increased 2 per cent per year and per-capita consumption of fish and fish products has increased from 42 pounds in 1950 to 62 pounds in 1966. A conservative estimate, based on population projections, income, and per-capita consumption is that total utilization of fish and fish products will increase 72 per cent from the current 6 million tons to 10.5 million tons by the year 2000 A.D.

If an industrial revolution in the sea takes place in the next 20 years—and we intend to show that this is our best possible prediction—then we can also predict reliably some of the charactertistics of this revolution. Conventional fishing will continue to develop, because of increased food needs and the availability of presently unharvested resources. Certain important fish products, such as shrimps and prawns, tuna, salmon, and a few prime varieties of groundfish, are at present riding high in world markets. These species will continue to be heavily exploited. Adoption of economic management policies for these species will be accomplished slowly. In the meantime, we must think in terms of more economical and efficient fishing vessels.

The increasing size, complexity, and cost of each unit of fishing vessels and gear make it doubly necessary to apply the best available design and operation research techniques to all aspects of a fishing enterprise. Technological advances must be made in catching, processing, handling, product development, and marketing. Costs are rising and margins of profits are decreasing.

Pressure of fishing effort has led to a general fall in catch/day at sea. Competition in the food industry has intensified. The need for lower cost production to meet the competition from other commodities is countered by rising unit costs and reduced fishing productivity on traditional fishing grounds. Any decision to invest in today's costly boats and gear, however, must be based on a conclusion that there are and will be stocks to be fished at a profitable level.

In addition to conventional fishing there will be new technology developed which will make economically possible several new lines of exploiting the oceans. The technological revolution, which has enabled us, using methods of scientific agriculture, to feed more people with less labor than ever before, will bring about similar changes in ocean exploitation.

We stand in urgent need of a technical breakthrough in the development of a low-priced fish product for human consumption which can be produced from quantities of raw material at least as great as those of the anchoveta and other fish now used for industrial purposes. An odorless and tasteless high-quality protein concentrate can be used in a wide variety of food products and gives hope for an entirely new use for a portion of the world's fishery resources. We will hear more of this today.

The present rate of expansion of world fishing cannot be maintained much longer on the types of fish now preferred. Really substantial increases in fish supplies must make use of species presently ignored. These smaller non-preferred fish are likely to be used for fish meal and similar products.

Florida, in particular, is in a fortunate position for expansion of the seafood and drug industries. With many miles of shoreline and a large continental shelf, valuable marine resources are close by. These include (1) the shrimp fishery—which in the South Atlantic and Gulf Area in 1967 exceeded 150 million pounds. The U. S. shrimp fishery is the first fishery in the United States to exceed $100 million dockside value. (2) A large industrial fish fishery for menhaden and in this last year, thread herring, on the west coast of Florida. This latter fishery has the potential for considerable expansion. (3) Scallop and deep water shrimp resources off the east coast of Florida have been known for some years and were recently resurveyed from the ALUMINAUT and were tested commercially by U. S. Department of Interior BCF exploratory fishing vessels. (4) Fish cannery in Miami —Florida's first such venture—fish canning recently undertook a quarter-million dollar project to develop canned products from Spanish mackerel and other species locally available.

Action

The food industry is an important one in the United States and, as population increases, will continue to be so. We need to ask ourselves how rapidly our present methods of gathering food from the sea will disappear? How outmoded are they? How competitive are the alternatives—aquaculture, and harvesting food of lower tropic levels? How rapidly can we learn to use other products—such as drugs—from the sea?

The food and drug industries themselves have recognized this need and consequent opportunity for growth. Some of the leading companies are already actively engaged in developmental projects to further tap ocean resources. These industries will develop only with careful thought.

It will require cooperation between research and education, industry, and government—research and education to supply the knowledge, industry to implement knowledge in an aggressive, efficient manner, and government to create the climate for an economically prosperous and healthy operation.

Today federal spending represents a relatively large part of the total ocean budget. Federal spending is based on the premise that it will prime the pump for a greatly expanded private, competitive, free enterprise market. We have seen a number of industries grow, with the support of government—for example, the air industry developed with the guidance of the National Advisory Committee for Aeronautics. I predict that the ocean industry will grow in a similar way with the support of a similar government agency.

In summary, we need to do four things to stimulate the utilization of the living resources of the sea.

1. Develop new techniques for increasing yields from the ocean (aquaculture).
2. Streamline our methods of locating and catching fish and other living resources of the sea to compete more effectively with other countries in the race on food.
3. Remove the institutional barriers that would hamper harvesting the resources at the lowest cost. These barriers include conflicting state laws and restrictions of efficient fishing gear in the name of conservation.
4. Further development of new products (such as FPC and drugs) which will utilize species not presently exploited.

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NOTES AND NEWS

LEPAS ANSERIFERA LINNÉ (CIRRIPEDIA LEPADOMORPHA) FEEDING ON FISH AND *PHYSALIA*

BY

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Until Howard & Scott (1959) observed predatory, macrophagous behavior of goose barnacles, those crustaceans were generally considered to feed on small organisms and detritus by sweeping the water with their cirri. 1)

This paper reports *Lepas anserifera* feeding on young flying-fish and on the siphonophore *Physalia.* An associative feeding behavior among the barnacles and mutualism between the barnacles and the pelagic snail, *Ianthina* sp., to which they were attached are suggested.

In our first example of predation by the barnacle in 1956, several specimens of *Ianthina* with attached barnacles were dip-netted from the surface water near long. 110° W, lat. 13° S, during cruise 38 of the "Hugh M. Smith", research vessel of the U.S. Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii. The animals were placed in an aquarium for observation, together with three or four young flying-fish (Exocoetidae) about 5 to 10 mm long. The fish soon began to swim upside down in distress near the surface. When this behavior brought a fish near to or into contact with the cirri of a barnacle, it was seized and quickly manipulated until the caudal end was held between the mouth parts of the barnacle. Intermittent observations were continued about 2 hours. During that time, on several occasions, a partially consumed fish was observed to be withdrawn from the mouth parts and held in the tips of the extended cirri. At the same time, the barnacle began to swing in arcs by bending the flexible peduncle. When the fish contacted an adjacent barnacle, that barnacle grabbed it and the apparently satiated one released its hold. Repetition of this sequence resulted in the fish being passed from barnacle to barnacle until it was consumed. These observations suggest that the behavior within *Lepas* colonies results in a more nearly complete utilization of items of food which are too large to be consumed by one barnacle.

In the second example, on April 10, 1964, a living *Ianthina* with attached

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1) While this note was in press R. Bieri has published a similar account of *L. anserifera* feeding on large organisms (Publ. Seto mar. Lab., **14** (2): 161-170. 1966.)

Lepas was picked up from the beach of Kailua Bay, Oahu, Hawaii, along with several living specimens of *Physalia*. These were placed in a 50-gallon sea-water aquarium. Surface-water movements set up by the filter system soon caused the snail and one of the *Physalia* to drift together. The barnacles immediately seized the pendant polyps of the *Physalia* and began to ingest them. The barnacles near the bottom of the cluster seized the longer dactylozooids (pl. I fig. 1), while others nearer the surface fed on the shorter digestive and reproductive polyps. Within a few minutes, the snail began to feed on the pneumatophore and the shorter polyps (pl. I fig. 2). Within 48 hours the *Ianthina* and the barnacles ate all or most of six *Physalia* which had pneumatophores ranging from 20 to 40 mm long. Bayer (1963) reported that a single *Ianthina* consumed a much larger *Physalia* within 1 day. Attempts to free the *Physalia* by pulling it away along the surface of the water caused the *Ianthina* to lose its hold, but the barnacles retained their grasp while the colony was towed rapidly several times the length of the aquarium.

The presence of the cluster of *Lepas* on the snail may be advantageous to the snail in the procurement of food. For example, the barnacles, extending in many directions around the shell, contact potential food in a volume of water greater than that within the snail's sweep. The barnacles may secure large prey such as *Physalia* against being blown or washed away by wind or waves. The contribution of the snail to mutualism appears to be only that of providing a substratum, and there is no evidence that *Lepas anserifera* prefers the shells of *Ianthina* over other available floating objects such as pumice, wood, or glass.

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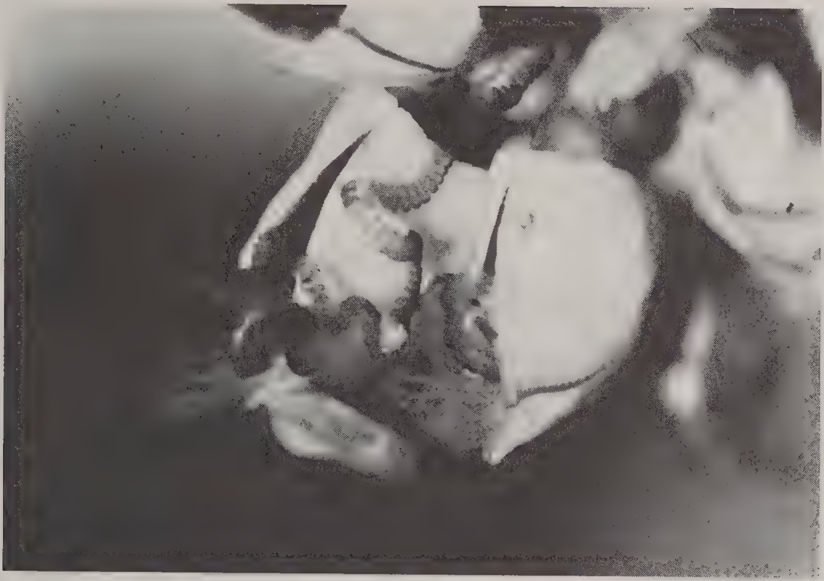

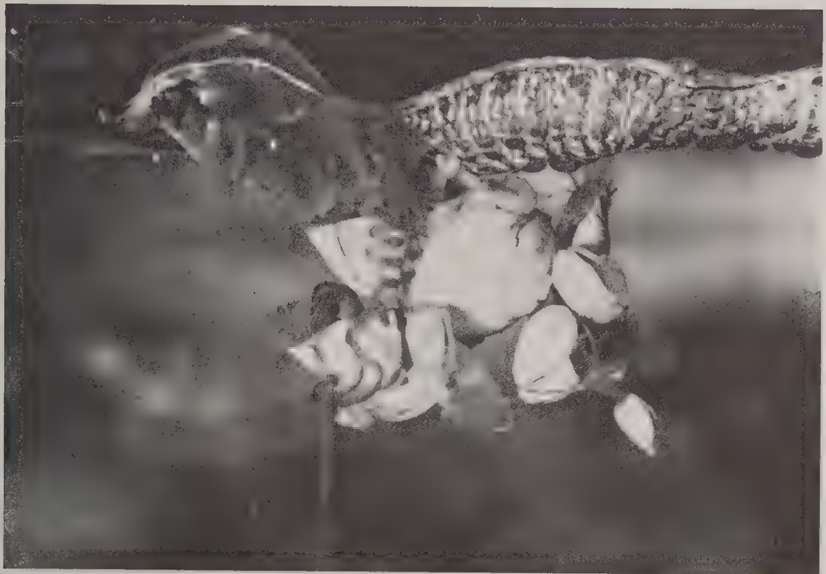

Fig. 1. *Lepas anserifera* L. feeding on the dactylozooids of *Physalia.*

Fig. 2. *Lepas anserifera* L. and *Ianthina* sp. feeding on the pendant polyps and the pneumatophore of *Physalia.*

A NEW SPECIES OF *TORTANUS* (CALANOIDA) FROM PAGO PAGO HARBOR, AMERICAN SAMOA

BY

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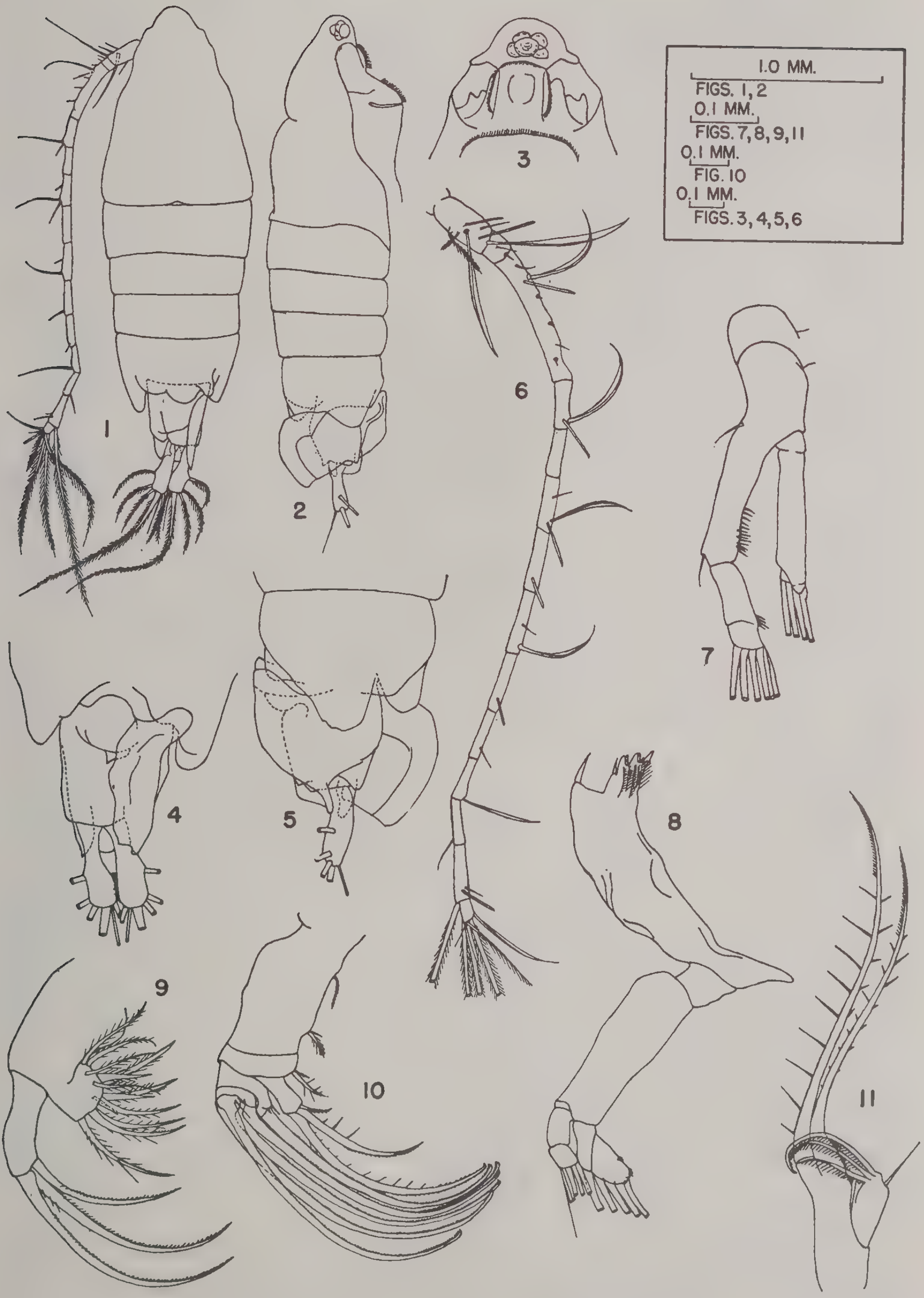
Plankton samples have been collected from time to time by personnel of the U.S. Bureau of Commercial Fisheries Biological Laboratory, Honolulu, in lagoons and neritic waters of many of the oceanic islands of the Pacific. Samples collected in Pago Pago Harbor, American Samoa, during visits of the Laboratory's research vessels, contained an undescribed species of *Tortanus* which is described here. The samples were collected around submerged lights at night, and therefore the composition of the samples may not reflect the true relative numbers in the plankton community. The individuals of *Tortanus* were rare; the predominant copepod was *Undinula vulgaris* (Dana).

This description brings to 15 the known valid species of *Tortanus: T. gracilis* (Brady, 1883) and *T. barbatus* (Brady, 1883); *T. recticauda* (Giesbrecht, 1889) and *T. forcipatus* (Giesbrecht, 1889); *T. discaudatus* (Thompson & Scott, 1897); *T. setacaudatus* (Williams, 1906); *T. murrayi* A. Scott, 1909 and *T. brevipes* A. Scott, 1909; *T. tropicus* Sewell, 1932; *T. derjugini* Smirnov, 1935; *T. longipes* Brodsky, 1948; *T. spinicaudatus* Shen & Bai, 1956; *T. compernis* González & Bowman, 1965 and *T. rubidus* Tanaka, 1965. The new species is named in honor of the late Dr. W. Giesbrecht.

Tortanus giesbrechti sp. nov.

Localities and materials. — Pago Pago Harbor, American Samoa: Cruise 8 of the R.V. "Hugh M. Smith", collected by J. E. King around a submerged night light, 2150-2250 hours local time, 22 February 1951; six females, one male. Cruise 55 of the R.V. "Charles H. Gilbert", station 105, collected by C. J. Rollet around a submerged night light, 15 March 1962; eight females.

Types. — Type material has been deposited in the United States National Museum as follows: female holotype from cruise 8 (USNM 119158), five female paratypes from cruise 8 (USNM 119160), male allotype from cruise 8 (USNM 119159).


1.0 MM.
FIGS. 1, 2
0.1 MM.
FIGS. 7, 8, 9, 11
0.1 MM.
FIG. 10
0.1 MM.
FIGS. 3, 4, 5, 6
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Figs. 1-11. *Tortanus giesbrechti* sp. nov. 1, dorsal view; 2, right lateral view; 3, head, ventral view; 4, fourth and fifth thoracic segments and abdomen, ventral view; 5, fourth and fifth thoracic segments and abdomen, left lateral view; 6, first antenna; 7, second antenna; 8, mandible; 9, first maxilla; 10, second maxilla; 11, maxilliped.

Measurements of total length were made from the anterior margin of the head to the end of the longer caudal ramus. The cephalothorax of the female was measured from the anterior margin of the head to the space between the left and median lobes of the posterior margin of the fifth thoracic segment, and the length of the abdomen from the anterior margin (dotted line, fig. 1) to the end of the right ramus. The measurements of the abdominal segments of the male included the telescoped portions indicated by dotted lines in fig. 20. These telescoped portions were not included in the cephalothorax-abdomen ratio of the male.

Description. — Female. The total length of the holotype was 2.57 mm. The range for five paratypes was 2.64 to 2.70 mm. The cephalothorax-abdomen ratios of the holotype and one paratype were 3.15 : 1 and 3.00 : 1. The cephalothorax is slender with a length-width ratio of about 2.7 : 1. The head is separated from the first thoracic segment and narrows anteriorly to a prominent rounded forehead containing an internal multilobed eye (figs. 1, 2).

In lateral view the head has a prominent sulcus in the dorsal margin just anterior of the midpoint of that margin. The frontal organ is low and the rostrum is absent (figs. 2, 3).

The fourth and fifth thoracic segments are fused. The fifth thoracic segment, in dorsal view, has four posterior lobes: the left one is longest, the median one is rounded and slightly right of the midline, the right lobe is equal in length to the median, and there is a short, acute lobe between the right and median lobes. The abdomen consists of two segments. Segments 1 to 4 are fused and the anal segment is fused with the caudal furca. In all 15 females, the abdomen bore extensive chitinous processes. An attempt to remove them with dissecting needles from one female failed, but in spite of this failure and the lack of variation in the form of these processes, it is possible that they are accessory spermatophoric material such as is found in the Pontellidae and Acartiidae. The most prominent characters of these processes are two large vanes on the right and left of the genital region, lying in sagittal planes. The right vane extends more dorsad than ventrad; the left extends more ventrad than dorsad (figs. 2, 5). The caudal edge of both vanes reaches to a line that includes about 50 percent of the length of the caudal rami but the right is slightly longer. The anterior edges of the vanes fit into notches in the fifth thoracic segment.

The caudal rami are 3 times as long as wide, nearly symmetrical, and bent to the left in dorsal view (fig. 1). The distal portion of the internal margin of each ramus bears a patch of fine hair. Each ramus bears six setae; the fourth from the outside is about 3 times the length of the others. The fifth is a minor non-plumose seta.

The first antenna (fig. 6) reaches to the middle of the abdomen and is composed of 14 free segments. The anterior edge bears several distinctive curved setae that have narrow membranes on the concave margins.

The endopod of the second antenna (fig. 7) is longer than the exopod, is fused with the basipod, and terminates in two partially fused segments which are

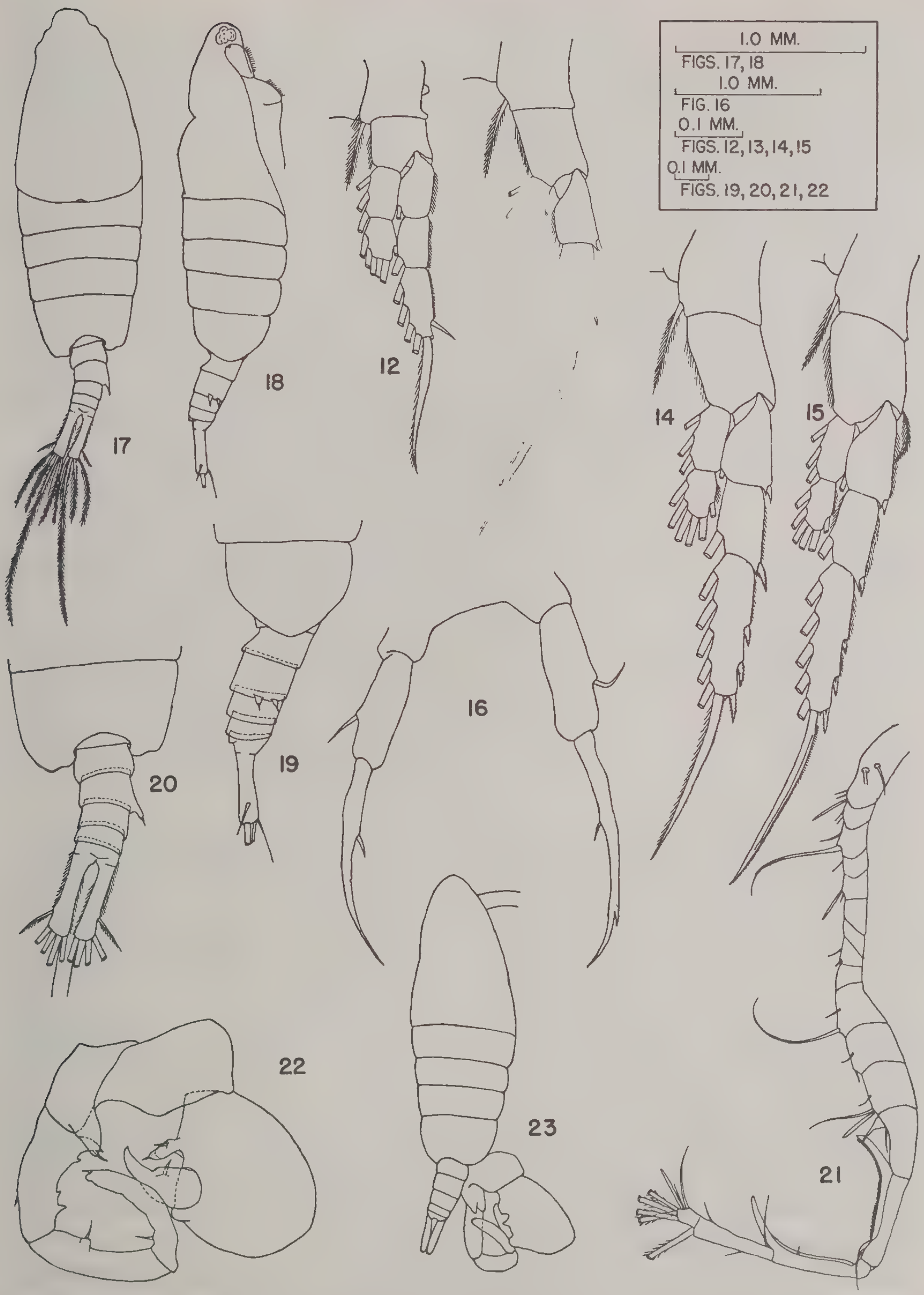
1.0 MM.
FIGS. 17, 18
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FIG. 16
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FIGS. 12, 13, 14, 15
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FIGS. 19, 20, 21, 22
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Figs. 12-23. *Tortanus giesbrechti* sp. nov. 12-16, adult female. 12, first foot; 13, second foot; 14, third foot; 15, fourth foot; 16, fifth feet. 17-23, adult male. 17, dorsal view; 18, right lateral view; 19, fourth and fifth thoracic segments and abdomen, right lateral view; 20, fourth and fifth thoracic segments, dorsal view; 21, right first antenna; 22, fifth feet, posterior view; 23, sketch of male showing relative size of male fifth feet.

not distally lobed. There are six apical setae, a single seta on the disto-lateral margin of the first segment and spinules are present on the internal margins of the first and second segments. An additional external seta is located at the disto-lateral corner of the fused basipodal segment. The exopod is separated from the basipod, consists of three partially fused segments, and has four apical setae. The first basipodal segment extends medially as a rounded prominence.

The outer point of the mandibular blade (fig. 8) is an articulated spine and is separated from the other points by a wide diastema. The remaining grouped armament consists of a short articulated spine; two blunt bifid processes; a small tooth; and a sharp spinous process. Five rows of fine spinules are proximal to these grouped processes.

The first maxilla (fig. 9) is similar to that of other members of the genus and consists of two endopodal lobes, the proximal one with 13 spines and setae and the distal one with 3 long spines.

The second maxilla is composed of five basipodal lobes and three endopodal segments; the details are best described by reference to fig. 10.

The maxilliped (fig. 11) is similar to that of other members of the subgenus *Atortus* Sewell, 1932, in having only two long spines on the first segment.

The first swimming foot (fig. 12) has a small tooth on the external margin of the first basipodal segment. The external margin of the exopod bears one spine, which is located on the distal corner of the last segment. The long apical spine on this foot is plumose on the internal margin and finely denticulate on the external margin. The length of the apical spine is 1.9 times the length of the distal exopodal segment.

The first and second exopodal segments of swimming feet 2, 3, and 4 (figs. 13, 14, 15) have one external spine and the third segment has three external spines. The distal endopodal segments have six setae. The apical spines of swimming feet 1 to 4 have these lengths relative to the lengths of the distal exopodal segments: 2.0 : 1, 1.17 : 1, 1.28 : 1, and 1.15 : 1. The second basipodal segment of the fourth foot bears a plumose seta on the disto-lateral corner.

The fifth feet of the female (fig. 16) are long and slender, two-segmented, and asymmetrical. The length of the right foot is 1.14 times that of the left. The distal segment of the right foot has an external spinous process one-fourth of the segment length from the distal end and an internal spine two-fifths of the segment length from the proximal end. The left foot lacks the external process, and the internal spine is one-third of the segment length from the proximal end. Both distal segments curve slightly inward. Each of the proximal segments bears a single seta on the external margin.

Male. The total length of the allotype was 2.37 mm and the cephalothorax-abdomen ratio was 2.79 : 1. The cephalothorax (figs. 17, 18) is similar to that of the female except that the fifth thoracic segment in the male is not produced into prominent lobes. The corners of that segment are asymmetrical (figs. 17, 20); the left is slightly longer than the right. The abdominal segments are deflected to the left. The second abdominal segment bears two spinous processes on the right side (fig. 19) near the posterior margin, but only one of them is visible in dorsal view (fig. 20). The relative lengths of the abdominal segments were: 13.0, 20.3, 14.5, 11.6, 8.7, and 31.9 (furca) = 100. The caudal furca is partially fused with the anal segment. Its rami are asymmetrical; the left is slightly longer. Each ramus bears coarse hair on the internal and external margins and has six setae. The relative lengths of the setae, from lateral to medial, were: 4.8, 15.5, 15.4, 39.0, 9.8, and 15.5 = 100. The fifth from the outside is a minor non-plumose seta.

The right first antenna of the male (fig. 21) is strongly geniculate. The anterior margin of segment 18 has a pectinate, retroverse process which extends proximad almost the length of segment 17. The anterior margin of segment 17 has a peculiar spinous process with a bulbous base, as in *T. tropicus*. Segments 19, 20, and 21 are fused and bear a smooth, apectinate process similar in size and shape to that of segment 18. These two processes form the jaws of a grasping organ. Segments 13 to 17 are slightly swollen.

The fifth swimming feet (fig. 22) are very large and make up perhaps 20 percent of the volume of the entire copepod (fig. 23). The proximal (basipodal) segment of the right foot is swollen laterally and is without processes; the second segment is a thick, swollen ovoid on the inner margin of which is a thumb bearing two short setae. Distal to the thumb is the small third segment, which is clawlike and has smooth margins, a swollen base, and a single short seta. The curved claw of this segment is longer than indicated in fig. 22, which is foreshortened. The inner distal corner of the basipodal segment of the left foot has a triangular process with a single seta. The second segment has a single small seta on the external margin and four processes on the inner margin. The proximal process is largest and triangular; near its base is the second process which is small and slightly retrorse. The other two processes are near the distal end of the segment and are small and about equal. The third and fourth segments are narrow; the third bears a single seta on a raised process on the internal margin, and the fourth has a seta near the inner proximal margin and a single, very short, distal seta.

Remarks. — This new species of *Tortanus* from Samoa is most closely related to *T. longipes* Brodsky from Poset Bay, between latitudes 42° and 43° N in the Sea of Japan. Brodsky described only the male, but Tanaka (1965) described both sexes from the Izu region of Japan. The following details of the male fifth feet of *T. giesbrechti* distinguish it from Brodsky's species as figured by Tanaka (1965): the presence of a triangular process on the disto-medial corner of the basipodal segment of the left foot; and the presence of four processes on the medial margin of the second segment of the left foot. Brodsky (1950) stated that the caudal rami are symmetrical in *T. longipes*; in *T. giesbrechti* the left ramus is clearly longer than the right. The female of *T. giesbrechti* differs from that of *T. longipes*, as described by Tanaka (1965), in the shape of the urosome and posterior segments of the metasome; and, most notably, in the form of the fifth feet.

ZUSAMMENFASSUNG

Tortanus giesbrechti nov. sp. aus dem Seichtwasser um die Samoa-Inseln wird beschrieben. Das Männchen ähnelt *T. longipes* Brodsky mit Ausnahme der Besonderheiten des fünften Fusses und der Furka. Letztere ist asymmetrisch.

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ADDITIONAL RECORDS OF THE PEDUNCULATE BARNACLE, *CONCHODERMA VIRGATUM* (SPENGLER), ON FISHES

BY

EVERET C. JONES, BRIAN J. ROTHSCHILD and RICHARD S. SHOMURA

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Ciurea, Monod & Dinulesco (1933) noted that the direct attachment of barnacles to fishes is rare. They cited previous records of pedunculate barnacles on the following genera: *Mola, Gymnothorax, Serranus, Etmopterus,* and *Cetorhinus.* The present paper provides two records of the pedunculate barnacle *Conchoderma virgatum* (Spengler, 1790) on the suckerfish *Remora remora* (L.) and on the sailfish *Istiophorus orientalis* Schlegel. Ciurea et al. reported *Conchoderma virgatum* on *Mola rotunda* Cuvier, *Mola mola* (L.), and *Gymnothorax favigineus* Schneider. Sumner, Osburn & Cole (1913) reported *C. virgatum* from *Tylosurus acus* (Lacépède), and Crozier (1916) recorded it from *Diodon hystrix* L. No other records of this barnacle from fishes are known to us.

The first example of attachment of *Conchoderma* to a fish was observed during cruise 63 of the "Charles H. Gilbert" (January 23, 1963). Two suckerfish were removed from a great blue shark *Prionace glauca* (L.) caught by longline at 15° 53′ N, 149° 54′ W. Two *Conchoderma virgatum* were attached to the dentary region of one of the suckerfish (106 mm standard length, fig. 1). One of the barnacles was large relative to the size of the fish; the other was small (25 mm and 5 mm total length). The volume of the barnacles, estimated by water displacement, was about 10 percent of that of the fish.

The peduncle of the smaller barnacle was partially attached to the tissues of the fish and partially to the peduncle of the larger barnacle and, because small barnacles frequently attach to the peduncles of larger ones, it was probably there rather than on the fish that the cypris stage initially settled. The cypris of the larger barnacle apparently settled in or near the groove between the dentary and the articular portions of the mandible. The portion of the dentary adjacent to the point of attachment of the barnacle was distorted and the teeth there were either absent or covered with abnormal tissue. It was not possible without histological examination to distinguish the tissues of the barnacle completely from those of the fish, but it appeared that the barnacles had caused lesions which extended anteriad almost to the mandibular symphysis and posteriad to include the left eye of the fish. The cornea of that eye was opaque and flattened and the size of the pupil was greatly reduced. In other respects the general condition of the suckerfish

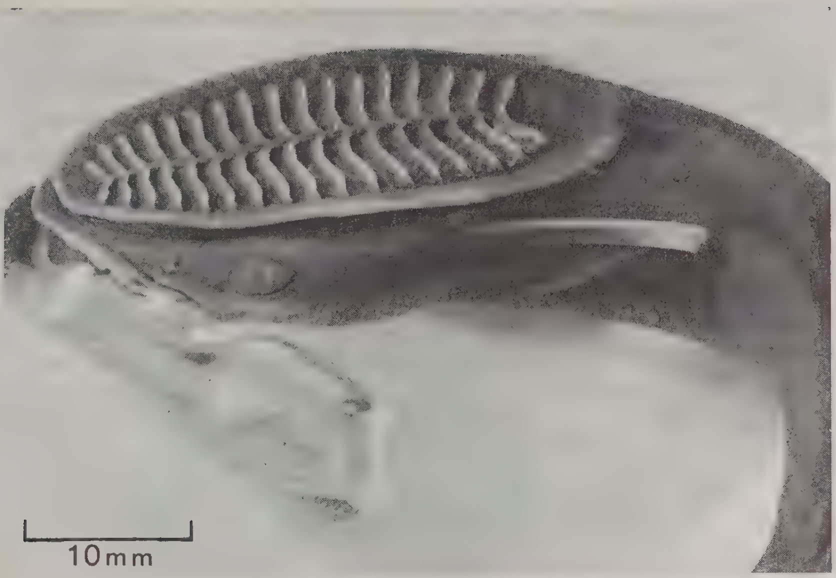

Fig. 1. Two *Conchoderma virgatum* (Spengler) attached to the dentary region of a suckerfish, *Remora remora* (L.).

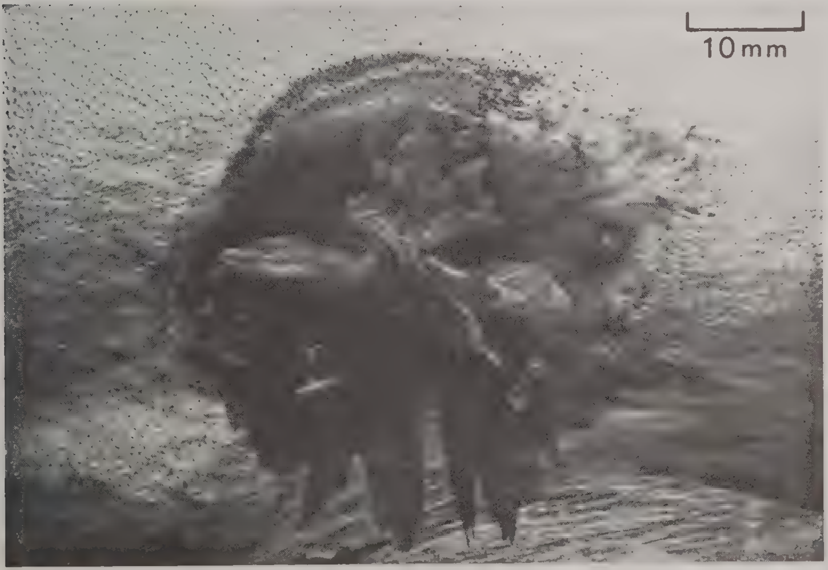

Fig. 2. A cluster of *Conchoderma virgatum* (Spengler) attached to a lesion on the side of a sailfish, *Istiophorus orientalis* (Schlegel).

appeared to be normal; apparently the presence of the barnacles was not a serious handicap in feeding.

Although the barnacles may have been the cause of the abnormal appearance of the tissues of the suckerfish, it is possible that a wound or abnormality existed there before the settling of the cypris. Crozier (1916) stated that when *C. virgatum* was attached to a spine of *Diodon* the skin at the base of the fish's spine was inflamed and the muscles associated with the spine were degenerated. Whether or not the larvae of *Conchoderma* can successfully attach to normal fish integument is open to question. Crozier (1916) was of the opinion that "those occurring on fishes seem, naturally, to affix themselves to some hard part". *Conchoderma virgatum* has been reported most often attached to the various species of the copepod genus *Penella,* which is parasitic on a variety of high seas fishes as well as on the blue whale. *Conchoderma virgatum* has also been reported attached to two other genera of parasitic copepods, to its congener *C. auritum* (L.), and to sea snakes (Ciurea et al., 1933). These records suggest, on the one hand, that the species is an opportunistic settler; on the other hand, it has not been reported from such common floating objects as glass fish-net floats, pumice, feathers, or organisms such as *Velella* and *Ianthina*, all of which are common substrata for *Lepas.* Although the integument of fishes as a substratum may be avoided by preference, it seems more likely that the cypris is usually unable to attach or to remain attached to fishes because of their mucous secretion.

The second example of barnacle — fish association was observed on July 6, 1963, during cruise 2 of the "Anton Bruun" during the International Indian Ocean Expedition. A sailfish (*Istiophorus orientalis*) 150 cm long was caught on longline gear at 06° 45′ S 69° 41′ E. On the left side, about 45 cm above the insertion of the first anal spine, a cluster of *Conchoderma virgatum* was attached to the tissues of the fish (fig. 2) in an elliptical craterlike lesion (25 mm dorsoventrad by 40 mm anteroposteriad). The wound was approximately 10 mm deep and filled with barnacles and with filaments of the fish's tissues. Just under the external lesion and extending mediad to the peritoneum was a large hard cyst. This cyst was also about 25 mm by 40 mm and 5 to 10 mm thick. Yamaguti (1963) stated that the parasitic copepod *Penella* "burrows through the skin and tissues and buries its head in some vital organ, forming an enormous cyst, which becomes very hard and remains for a long time after the death of the parasite." Thus it is likely that the original cause of the wound on the sailfish was the presence of one or more *Penella* and that the barnacles initially settled on that parasite and continued to do so until the copepod died. The largest of the barnacles was about 15 mm long. About 10 individuals longer than 10 mm were attached directly to the tissues of the fish and many smaller individuals were attached to the peduncles of the larger ones. Under magnification, several newly attached cypris larvae could be seen. Thus the colonization of the cirripeds on the fish, once initiated, was apparently continuous. If stubs of chitinous material remained after the copepods died, they would provide a substratum for additional barnacles and in time could have led to their attachment directly to the tissues of the fish. It seems doubtful, however, that *Penella* was a precursor of the barnacles attached to the remora. Yamaguti (1963) reported *Penella* from the suckerfish, but the suckerfish described here, gave no evidence of an internal cyst, and the place of attachment of the barnacles on the mandible was unlikely for *Penella*.

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ZUSAMMENFASSUNG

Es gibt nur wenige bisher bekannte Fälle eines Anheftens von Cirripedien an Fischen mittels des Pedunculus. Im vorliegenden Bericht werden zwei zusätzliche Fälle geschildert. Der erste Fall betrifft die Anheftung von *Conchoderma virgatum* an *Remora remora* in den Gewässern um Hawaii, der zweite die Fixierung von *C. virgatum* an *Istiophorus orientalis* im Indischen Ozean. Die Art und Weise der Fixierung und die Beziehung der Cirripedien zum Fisch werden kurz erörtert.

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Triakis acutipinna (Galeoidea, Triakidae), a New Species of Shark From Ecuador

SUSUMU KATO

Triakis acutipinna **is distinguished from all other species of the genus by the following combination of characters: lower lobe of caudal fin expanded, with a sharply pointed tip; most fins with white tips, all with sharp tips; snout ovate viewed from above; teeth erect or only slightly oblique; teeth spikelike, a few upper teeth with a secondary cusp on each side of the main cusp, but most with only one secondary cusp on the lateral side (the presence of secondary cusps may be a variable character); lower teeth unicuspid. New data are given for several inadequately described species, and relationships among the genera** ***Calliscyllium, Eridacnis, Mustelus, Neotriakis, Rhinotriacis,*** **and** ***Triakis*** **are discussed.**

INTRODUCTION

THE genus *Triakis*, as defined by Bigelow and Schroeder (1948), includes smoothhounds that lack barbels, have nostrils separated from the mouth, teeth compressed with one larger sharp cusp flanked by one or more smaller cusps on either or both sides, conspicuous labial grooves and spiracles, and other characters common to the Triakidae.

Seven species of *Triakis* were recognized by Bigelow and Schroeder (1948), who followed Garman (1913), Fowler (1941), and others in synonymizing *Rhinotriacis* Gill 1862, *Calliscyllium* Tanaka 1912, and *Hemitriakis* Herre 1923 with *Triakis* Müller and Henle 1838. The seven are: *leucoperiptera* Herre, 1923; *scyllia* Müller and Henle, 1838; and *venusta* Tanaka, 1912, all from the western Pacific; *henlei* Gill, 1862; *maculata* Kner and Steindachner, 1867; and *semifasciata* Girard, 1854 from the eastern Pacific; and *barbouri* Bigelow and Schroeder, 1944 from the western Atlantic. Subsequently Garrick (1954) described an eighth species, *T. attenuata*, from New Zealand, and Smith (1957) described a new genus and species, *Neotriakis sinuans*, probably referable to *Triakis*, from South Africa.

In October 1961, a party on the University of Miami R/V ARGOSY collected, at Isla de la Plata, Ecuador, a single specimen of an undescribed species of shark referable to *Triakis*. The specimen, an adult or subadult female, is described below.

Methods of measurements followed those used by Bigelow and Schroeder (1948). Calipers were used whenever possible, but

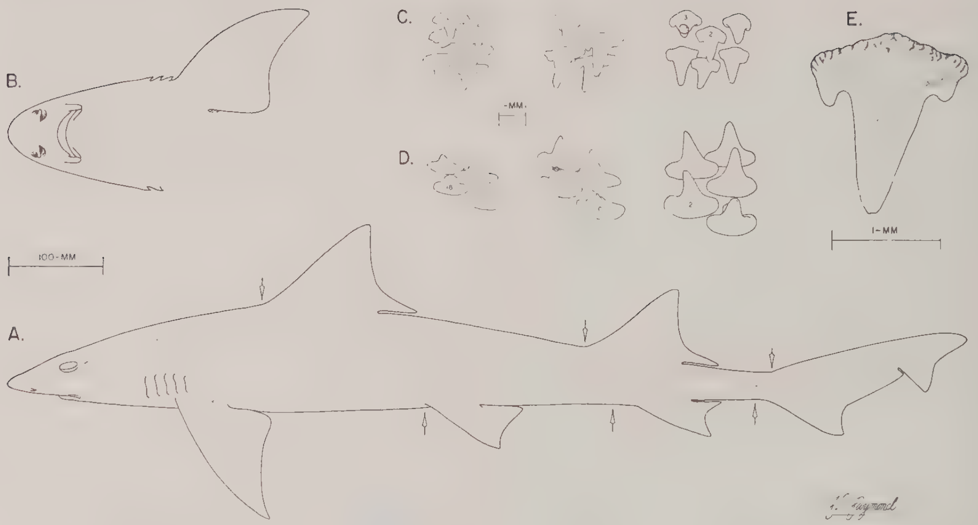

Fig. 1. *Triakis acutipinna* n. sp. A. Lateral view. B. Ventral view of head. C. Upper teeth on right side of jaw; numbers on teeth refer to the position of the teeth in the jaw (1 = center of jaw). D. Lower teeth on right side of jaw. E. Upper tooth, sixth row. (All drawings of teeth were made with the aid of a camera lucida.)

because of the bent shape of the specimen, a string was used to estimate some of the dimensions.

Triakis ***acutipinna*** n. sp.
(Figs. 1, 2)

Holotype, U. S. National Museum 201409, female 1018 mm total length; captured by fishermen at Isla de la Plata, Ecuador; and acquired by the staff of the R/V ARGOSY (specimen No. 84); 10 October 1961.

Description.—Proportional dimensions as percentages of total length: trunk at pectoral origin: width 11.0, height 9.2; least depth, caudal peduncle: 2.8; eye: horizontal diameter 2.2, vertical diameter 1.1; interorbital distance: 6.1; mouth: width 4.9, length 1.8; nostrils: distance between inner ends 2.6; length of labial grooves: outer 2.0, inner 1.5; gill slit lengths: 1st 2.4, 2nd 2.4, 3rd 2.4, 4th 2.2, 5th 1.6; first dorsal fin: vertical height 9.0, base 12.0, free rear tip 4.3, anterior margin 13.8; second dorsal fin: vertical height 7.7, base 10.2, free rear tip 4.0, anterior margin 11.4; anal fin: vertical height 3.6, base 8.3, free rear tip 3.2, anterior margin 10.8; caudal fin: upper margin 20.4, lower anterior margin 10.0, tip to notch 6.6, depth of notch 3.5; pectoral fin: anterior margin 15.7, distal margin 10.8, inner margin 4.5, base 5.5; pelvic fin: anterior margin 9.4, distal margin 6.7, base 6.1, overall length 10.4; distance from snout to: outer nostrils 2.6, eye 5.4, mouth 5.1, 1st gill slit 14.5, 5th gill slit 18.9, 1st dorsal 26.5, 2nd dorsal 60.3, upper caudal 79.2, pectoral origin 17.5, pelvic origin 43.4, cloaca 46.4, anal origin 63.1; space between bases of: 1st and 2nd dorsals 21.8, 2nd dorsal and caudal 8.6, pectoral and pelvic 20.4, pelvic and anal 13.6, anal and caudal 5.7; distance from origin to origin: pectoral and pelvic 25.9, pelvic and anal 19.6.

Snout depressed, broadly ovate at tip (Fig. 1, A and B). Body robust, gradually elevated to first dorsal fin, tapering gently from that fin to caudal base; distance from snout tip to cloaca shorter than from cloaca to tip of caudal. Depth at pectoral origin 8.6 times in length to caudal base. Caudal peduncle somewhat compressed; keels and precaudal pits absent; least depth of peduncle slightly greater than height of third gill slit. Lateral line running from above eyes onto upper caudal lobe, marked with small white spots. Ridge on mid-dorsum extending from above first gill slit to caudal base, interrupted by dorsal fins.

Head length measured to last gill slit 5.3 times in total length; shorter than space between bases of dorsal fins. Head broad; least interorbital distance 3.1 in head; snout moderately long, distance between tip and front of eye 3.5 in head. Snout in front of mouth equal to mouth width. Nostrils oblique, distinct from mouth; anterior margin with fingerlike lobe, rounded at tip; distance between inner ends of nostrils equal to length of snout in front of outer ends and 7.4 times in head. Eyes dorsolateral, slanted; horizontal diameter 2.8 in interorbital, 2.4 in snout in front of mouth. Nictitans poorly developed; lower lid long, reaching level of posterior margin of eye, continuous anteriorly with upper lid, attached to nictitans, posterior end free. Spiracles tiny slits, located about half eye diameter behind eyes. Mouth rounded; width 3.8 and length 10.7 in head. Long labial grooves at corners of mouth; outer grooves longer, 1.1 in horizontal diameter of eye. Gill slits slightly arched, first four of nearly equal height, slightly longer than eye; last gill slit notably shortest; last two gill slits located over pectoral base. Conspicuous pores on dorsal and ventral sides of snout.

Space between dorsal fin bases greater than length of head to last gill slit, about 3.6 times in body length to caudal base. Distance between origins of pectoral and pelvic longer, three times in body length.

First dorsal fin origin (including fleshy base) slightly ahead of inner rear corner of pectoral fin; length of base 1.6 times in head, vertical height 2.1 in head and 1.3 in base; anterior margin nearly straight; apex sharply pointed; posterior margin concave, abruptly vertical from the apex; free rear tip narrow, 2.1 in vertical height.

Origin of second dorsal fin (including fleshy base) behind tip of pelvic fin by a distance about equal to width of pelvic base; similar in shape to first dorsal but 0.85 times as high; posterior margin abruptly vertical from the apex, which is located directly over the posterior end of the base.

Fleshy base of anal fin originates under first third of second dorsal fin base, but abrupt rise of anterior margin starts under middle of second dorsal base; vertical height 2.3 times in anal base, and about half as high as second dorsal; base 1.2 in second dorsal base; anterior margin nearly straight, apex pointed, posterior margin deeply concave; free rear tip 1.1 in vertical height, terminating slightly posterior to tip of second dorsal.

Caudal fin five times in total length; upper lobe with slightly convex dorsal margin, subterminal notch deep; lower lobe well defined, anterior margin slightly convex, rear tip sharply pointed.

Pectoral fin origin slightly ahead of fourth gill slit; base 3.4 times in head; anterior margin convex, length nearly three times greater than base, tip sharply pointed, reaching to about level of middle of first dorsal base when laid back; distal margin concave; free inner margin shorter than base, rounded at rear corner.

Pelvic fin origin slightly behind rear tip of first dorsal fin; length of base 1.5 times in anterior margin and 3.1 in head; anterior margin nearly straight; distal margin slightly concave; free inner margin shorter than base, rear corner not narrow and elongate.

Teeth (Fig. 1, C–E) about 50/40, only slightly compressed, distal half of main cusps nearly elliptical in cross-section; no serrations on cusps; striations prominent at base in front of upper teeth but faint in lower teeth; arrangement of tooth rows (from outermost functional tooth to innermost replacement tooth) predominantly anteroposterior, but becoming increasingly oblique toward angle of jaw; obliqueness more pronounced in lower jaw. Upper jaw with two small central teeth; 3rd–15th teeth (from center of jaw) of similar size, 16th through 25th teeth progressively smaller; four series functional in front, three at side and near angle; teeth erect or slightly oblique; most central teeth with larger main cusp flanked at the base by small sharp or worn secondary cusp on one or both sides (the secondary cusps may be a variable characteristic); lateral teeth somewhat asymmetrical; medial side (i.e., toward the center of the jaw) slightly oblique; lateral side straight, usually with a notch and low secondary cusp at base; a few lateral teeth with a secondary cusp on each side of main cusp; teeth near angles of jaws small, without secondary cusps. Size of teeth in lower jaw similar from center to 5th tooth, becoming progressively smaller toward angle; central teeth about twice as large as opposing upper teeth; five or six series functional in front and sides, four near angle of jaw; most teeth slightly oblique; some central teeth symmetrical, others with concave inner margin and straight outer margin, with or without notch at base, but never with sharp secondary cusp; lateral teeth smaller, similar in shape to concave central teeth; teeth near angle of jaw with pronounced concavity on

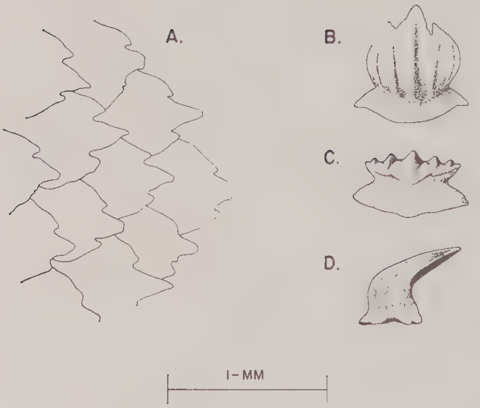

Fig. 2. *Triakis acutipinna* n. sp., camera lucida drawings of dermal denticles from slightly below base of first dorsal fin. A. Dermal denticles to show spacing. B. Top view of isolated denticle. C. Apical view. D. Lateral view.

inner margin; outer margin concave or straight, sometimes with notch at base.

Dermal denticles (Fig. 2, A–D) small, imbricate; denticles from high on back below base of first dorsal fin typically with rhomboidal base, short pedicel, and horizontal blade; most blades tridentate—a longer axial tooth flanked by a smaller tooth on each side; one or two (usually two) prominent ridges on each side of strong central ridge. Denticles on anterior dorsal margin of caudal fin closely packed, without ridges or teeth; denticles on sides below dorsal fin margin with strong ridges and teeth; intermediate denticles of intermediate shape; no space separating the different denticles.

Total number of vertebrae 176 (116 precaudal, 60 caudal); monospondylous vertebrae 46;

$$\text{“A” ratio } 123 \left(\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}} \times 100 \right);$$

$$\text{“B” ratio } 71 \left(\frac{\text{length penultimate monospondylous centrum}}{\text{diameter penultimate monospondylous centrum}} \times 100 \right).$$

Color in alcohol uniform brownish-gray on dorsal and upper lateral surface, fading to brownish-yellow on lower lateral and ventral surface; all fins slightly darker than body, and with a small patch of white at tips; distal margins of pectoral and pelvic and rear margin of anal fin edged with white; lateral line marked with tiny white spots.

Oviducts somewhat swollen, about two cm in diameter; probably adult or nearly so.

Comparisons.—*T. acutipinna* and *T. leucoperiptera* differ from all other species of the genus in having the lower part of the caudal fin expanded into a distinct lobe with a pointed tip, and fins with white margins (Herre, 1923). The following characteristics of *T. acutipinna* distinguish it from *T. leucoperiptera*: lateral teeth erect or slightly oblique with at most a single secondary cusp (teeth oblique, with as many as four secondary cusps in *T. leucoperiptera*); snout ovate viewed from above (somewhat pointed in *T. leucoperiptera*); teeth about 50/40 (18/34 in *T. leucoperiptera*; as Garrick (1954) pointed out, this count may be erroneous).

In addition to differences in shape of the lower caudal lobe and color of fins, sharks referred to *Triakis* can be separated from *T. acutipinna* by other characteristics. *T. barbouri* and *T. venusta* have the origin of the second dorsal fin over or behind the origin of the anal fin, and have short labial grooves (Bigelow and Schroeder, 1948). *N. sinuans,* which I refer to *Triakis,* also shares these traits (Smith, 1957). *T. attenuata* is an unusually slender shark with a unique head-shape and large eyes (Garrick, 1954). *T. scyllia* and *T. semifasciata* have rather blunt snouts and distinctive coloration, whereas *T. henlei* has a sharply pointed snout and is plain brownish-gray (Garman, 1913; Kato *et al.,* 1967). *T. maculata* has a moderately long and somewhat rounded snout, and is often distinctively spotted with black (Kato *et al.,* 1967).

The name *acutipinna* refers to the sharp-tipped fins. The common name "sharpfin smoothhound" may be applied to this species.

RELATIONSHIPS AMONG SMOOTHHOUNDS

Attempts to show relationships among species of *Triakis* and allied genera have been hindered by poor or erroneous descriptions of species. Relationships among genera within the Triakidae are also difficult to assess because characters used to separate the genera are sometimes variable. The following discussion is presented to call attention to certain errors in the literature, and to add information on some incompletely described species, as well as to point out how this information bears on previous interpretations of relationships among species of smoothhounds.

Triakis is presently separated from *Mustelus* on the basis of differences in tooth structure. *Triakis* has compressed, sharply pointed, multicuspid teeth and *Mustelus* has rounded, blunt, unicuspid teeth. Although tooth shape adequately separates "typical" forms such as *T. scyllia* and *T. semifasciata* from *M. californicus* and *M. mento*, it fails to do so with other species. *Mustelus dorsalis* (Kato *et al.*, 1967) and *M. nigropunctatus* (Smith, 1952), for example, have sharp teeth with fairly high cusps. *T. maculata*, on the other hand, may have unicuspid or multicuspid teeth. Thus, Hildebrand (1946) considered *maculata* a species of *Mustelus*, and de Buen (1959) erected subgenera to accommodate both tooth types under *Mustelus*. The use of tooth shape as the character distinguishing *Mustelus* from *Triakis* raises a problem that is particularly relevant to the description of *Triakis acutipinna*. I have on hand an adult male specimen from Ecuador that closely resembles the female holotype of *acutipinna* in shape and color of fins, shape of dermal denticles, proportional dimensions of body parts, vertebral characters, and number of teeth. The only clear difference is that the teeth of the male specimen lack secondary cusps; otherwise the teeth are similar to those of the holotype. Under the present concepts of the genera, the male specimen would be referable not to *Triakis* but to *Mustelus*. Although I feel that the difference in tooth shape is due to individual or sexual variation, an adequate series of specimens is needed to clarify the relationship between the two specimens. Until more specimens are available, the description of tooth shape in *T. acutipinna* must be considered incomplete, and the generic allocation tentative.

Bigelow and Schroeder (1948) and Garrick (1954) used external characters to indicate relationships among species of *Triakis*. Their data on eastern Pacific forms, however, were taken from a small sample and were not representative of all ages, and individual variations were not considered. For example, *henlei* and *maculata* were set apart from others of the genus because their upper teeth were reportedly blunt, with short major cusps. This statement may be true for some small specimens of *maculata* (Bigelow and Schroeder, 1940), but some, if not most larger ones have a single rather high and sharp cusp. The teeth in two jaws of adult Peruvian specimens at hand (about 150 and 175 cm total length) are unicuspid and high. Teeth in 13 jaws of *henlei*, 75–91 cm total length, from southern California also have main cusps that are sharply pointed, and notably longer than the secondary cusps. The number of cusps in these specimens varies from one to three. Bigelow and Schroeder (1948) reported that the dermal denticles of *henlei* and *semifasciata* were simple and lanceolate, but specimens I examined have strongly sculptured denticles. In *semifasciata*, most denticles are tridentate rather than lanceolate, but in *henlei* individual variation is greater. Most specimens of *henlei* have at least some tridentate denticles, and in a few this type predominates.

Differences in the mode of development in species of *Triakis* suggest that the genus as recognized by Bigelow and Schroeder (1948) is heterogeneous. Of the four species for which the mode of development is known, *semifasciata* and *barbouri* bear live young and have no placental attachment (Eigenmann and Eigenmann, 1889; Bigelow and Schroeder, 1948); *henlei* also bears live young, but has a placenta (Eigenmann and Eigenmann, 1889); and *venusta* is oviparous (Tanaka, 1915). Two other species, *leucoperiptera* (Herre, 1923) and *attenuata* (Garrick, pers. comm.) bear live young, but the mode of development is not known.

Smith (1957) attempted to rectify the apparent heterogeneity by splitting *Triakis* as defined by Bigelow and Schroeder (1948) into three genera: *Calliscyllium* (monotypic, *venustum*); *Neotriakis* (including *barbouri* and *sinuans* Smith, 1957); and *Triakis* (presumably including all other recognized species of *Triakis*, except *henlei*, which Smith implied was referable to *Mustelus*). The chief diagnostic character of *Neotriakis* is, according to Smith (1957), the lack of a nictitating membrane, which in the triakids has often been termed a "subocular fold" (Gilbert and Oren, 1964). Bigelow and Schroeder (1944) stated clearly, however, that a subocular fold was present in *barbouri*.

The question of whether or not a fold is present may be one of definition, or the character may be variable or affected by condition of preservation. Thus, although *sinuans* and *barbouri* are indeed similar in many respects, I consider the genus *Neotriakis* untenable, and provisionally regard *sinuans* as a species of *Triakis*.

Tanaka (1912) intended that *Calliscyllium venustum* be related to the Scyliorhinidae. Garman (1913) and several later workers (Fowler, 1941; Bigelow and Schroeder, 1948), however, referred *venustum* to *Triakis*, apparently because the forward position of the first dorsal fin, as found in *venustum*, does not occur elsewhere in the Scyliorhinidae. Tanaka (1915) refuted Garman's (1913) designation and pointed out that *venustum* was oviparous, a mode of development not found in any other species referred to the Triakidae. Further, Miyoshi (1943) showed that the cranium of *venustum* differed in many respects from that of *T. scyllia*. Thus, whatever the final familial designation of *C. venustum*, it seems clear that it does not belong in genus *Triakis*.

Gill's (1862) original description of *Rhinotriacis henlei* separated both his new genus and *Triakis* from *Mustelus*, which was characterized as having "teeth flat and paved." Gill further differentiated *Rhinotriacis* from *Triakis* on the basis of the shape of the snout and position of the first dorsal fin. Putnam (1863) synonymized *Rhinotriacis* with *Triakis* because of the similarity in tooth shape, although Gill (1862) did not make a point of this character in his treatment. Most later workers followed Putnam. Starks (1917) however, placed *henlei* in *Mustelus* with the proviso that if it were shown to have a placenta, it should be removed from that genus. Except for tooth shape, which is at best a variable character in *henlei*, as well as in species of both *Triakis* and *Mustelus*, *henlei* appears to be more closely allied to *Mustelus*, and I follow Starks (1917) and Smith (1957) in referring it to *Mustelus*. Supporting evidence is given by L. J. V. Compagno (pers. comm.) who finds that cranial characteristics of *henlei* are closer to those of *Mustelus* than to *Triakis*, in species that he examined (*M. californicus, M. higmani, M. lunulatus, T. scyllia*, and *T. semifasciata*).

The genus *Triakis* thus includes the following: *acutipinna, attenuata, barbouri, leucoperiptera, maculata, sinuans, semifasciata*, and *scyllia*. Further revision should take into account the mode of development and internal characters such as vertebrae and crania as well as external characters. Until this information is available, it seems wiser to take a conservative course and maintain the broad genus intact.

Smith (1913) described a new genus and species, *Eridacnis radcliffei*, from the Philippine Islands, basing its separation from *Triakis* on several characters. Most of these characters, however, are applicable to *barbouri* and *sinuans*, which were described later. The chief differences remaining which separate *radcliffei* from *barbouri* and *sinuans* are mouth shape and the alleged lack of labial grooves in *radcliffei* (Smith, 1913; Bigelow and Schroeder, 1948). A reexamination of the holotype by Victor G. Springer (pers. comm.) showed, however, that *radcliffei* had at least an upper labial groove, one mm long, or 0.4% of the total length. Although minute, the groove is similar in size to that of *barbouri*, which has an upper groove 0.5% of the total length (Bigelow and Schroeder, 1948). Thus *radcliffei* should probably be referred to *Triakis*, unless it can be shown to differ significantly in ways other than those proposed by Smith. *E. radcliffei* appears to be close to *barbouri* and *sinuans*. All three species have the following characteristics: forward position of the anal fin relative to the second dorsal fin; small labial grooves; long caudal fin; large eyes; small maximum size; and habitat in moderately deep water.

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NOTES ON FECUNDITY IN THE MARINE SPINY LOBSTER *JASUS EDWARDSII* (HUTTON) (CRUSTACEA: DECAPODA: PALINURIDAE)

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Summary

Fecundity in the New Zealand spiny lobster *Jasus edwardsii* (Hutton) has been investigated by a detailed examination of 14 selected females "in berry" (i.e. carrying external eggs), ranging in carapace lengths from 9.5 cm to 17.0 cm. The following data were obtained for each specimen: (a) the total weight of eggs carried, (b) the average number of eggs per 1 g sample, and (c) the total number of eggs carried.

A positive correlation was noted between the total weight of eggs carried and increase in carapace length. The total weight of eggs carried ranged from 26.9 g in a small specimen of 9.5 cm C.L., to 123.9 g in a large female of 16.0 cm C.L. No relation was found between the average number of eggs per 1 g sample and increase in carapace length. A low count of 3,541 eggs per 1 g sample was recorded, and a high count of 5,005 eggs. A direct relation was noted between the total number of eggs carried by *J. edwardsii* and increase in carapace length. The number of eggs carried ranged from a low figure of about 124,278 in a small specimen of 9.5 cm C.L., to a high figure of about 538,242 in a large female of 17.0 cm C.L. The rate of increase in fecundity was found to be greater in smaller than in larger females of *J. edwardsii*.

Introduction

Recently Kensler (1967a) published a paper on fecundity in *Jasus verreauxi* (H. Milne Edwards), the less common of New Zealand's two species of spiny lobsters or marine crayfish. The more common and widely spread "red spiny lobster", *Jasus edwardsii* (Hutton), is the subject of this study. In this paper fecundity refers to the reproductive potential of a female spiny lobster as estimated by the total number of eggs produced.

Holthuis (1963) has been followed with regard to the specific names of *Jasus* species discussed in the text, except for *J. verreauxi* which follows Kensler (1967b). Carapace length (C.L.) measurements only have been discussed in this study, and C.L. refers to the measurement taken along the mid-line between the base of the antennal platform and the posterior edge of the cephalothorax. All measurements have been recorded to the nearest 5 mm below (e.g. 10.0–10.4 cm, 15.5–15.9 cm).

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The literature concerning fecundity in spiny lobsters of the widespread Southern Ocean genus *Jasus* has already been reviewed in detail (Kensler 1967a). In 1935 von Bonde and Marchand studied fecundity in *J. lalandii* (H. Milne Edwards) from South Africa. Later Matthews (1962) in South West Africa, and Heydorn (1965) in South Africa made further egg counts of the same species. Fecundity in the Australian spiny lobster, *J. novaehollandiae* Holthuis, was examined by Hickman (1946) working in Tasmania. In New Zealand Bradstock (1950) obtained a few egg-count figures for *J. edwardsii* from the Wellington region; fecundity in *J. verreauxi* from northern New Zealand waters was studied by Kensler (1967a).

In his study, Bradstock (1950) did not specify the number of eggs carried by individual specimens of various sizes. In fact, the results of his investigation were not illustrated nor were the individual sizes of the 28 experimental females given. His results were stated as follows (1950, p. 17): " . . . the number of eggs carried by 28 crayfish (spiny lobsters) between 8.3 cm and 13.5 cm in carapace length ranged from 86,000 to 549,000." It is therefore not possible, from his published results, to determine the degree of correlation between fecundity and size of specimen. The present study has been undertaken to determine the fecundity of a wide size range of mature *Jasus edwardsii* females, as measured by the total weight of eggs carried, the average number of eggs per 1 g sample, and the total number of eggs produced.

MATERIALS AND METHODS

For the present study 14 female *J. edwardsii* "in berry" (i.e. carrying external eggs) and covering a wide range of carapace lengths from 9.5 cm to 17.0 cm (Table 1) were collected during mid October 1966 at the subantarctic Chatham Islands. The Chatham Islands are located at 44°S, 176°W (about 770 km east of New Zealand) and at present are the centre of New Zealand's large and valuable spiny lobster fishery (Kensler 1967c, and in prep.). The specimens were caught in pots, by commercial fishermen, in 40 to 70 m of water, deep frozen at the Chatham Islands while still fresh, and brought to the laboratory in Wellington for detailed examination.

The method employed for the present fecundity study was the same as that described for *J. verreauxi* (Kensler 1967a, p. 147): "The total egg mass was carefully removed from the pleopods of a fresh specimen, placed in fine plankton netting and gently squeezed to remove excess moisture. The egg mass was then weighed on a "Mettler P 120" balance having a guaranteed accuracy of 3 mg. Three 1 g samples of eggs were taken from an egg mass, were carefully counted (manually), and an average figure obtained for a 1 g sample from **that** particular egg mass." . . . "The average 1 g count for an egg mass . . . was then multiplied by the total weight of the egg mass to obtain the number of eggs carried by the female." This procedure, although arduous, was used to determine total egg counts for each of the 14 *J. edwardsii* specimens examined.

RESULTS AND DISCUSSION

The detailed results of the investigation are presented in Table 1. The following data are given for each of the 14 specimens examined: carapace and total length measurements, the total weight of eggs carried, the average number of eggs per 1 g sample (based on an average of three samples), and the total number of eggs carried.

TOTAL WEIGHT OF EGGS CARRIED

The total weight of eggs carried by *J. edwardsii* ranged from 26.9 g in a small female of 9.5 cm C.L., to 123.9 g in a large specimen of 16.0 cm C.L. (Table 1). A positive correlation is shown between the total weight of eggs carried and increase in carapace length (Fig. 1). The relation is slightly more pronounced in smaller than in larger females, as is indicated by the decrease in the slope of the curve with larger specimens i.e. females above 14.5 cm C.L. Variations in total weight of eggs carried are noted (Table 1) for specimens of the same 5 mm carapace length group (i.e. 14.0 cm and 15.0 cm). Kensler (1967a) found similar differences in *J. verreauxi* and suggested that the variations could be due to differences in respective total length and/or to individual variation in reproductive capacity.

TABLE 1—The carapace length and total length, total weight of eggs carried, average number of eggs per 1 g sample, and the total number of eggs carried, for each of the 14 *Jasus edwardsii* specimens examined

Size of specimen (cm)	Total weight of eggs (g)	Average number of eggs per 1 g sample*	Total number of eggs
1. 9.5 x 25.5	26.9	4,620	124,278
2. 10.0 x 27.0	38.2	3,541	135,266
3. 11.0 x 30.5	46.1	4,432	204,315
4. 11.5 x 32.0	59.4	4,287	254,648
5. 12.0 x 33.0	63.9	5,005	319,820
6. 12.5 x 34.0	68.6	4,568	313,365
7. 13.0 x 35.0	83.7	4,572	382,676
8. 14.0 x 37.5	92.4	4,573	422,545
9. 14.0 x 38.5	102.1	4,487	458,123
10. 15.0 x 40.0	114.5	4,142	474,259
11. 15.0 x 41.0	117.2	4,208	493,178
12. 15.5 x 40.5	110.8	4,693	519,984
13. 16.0 x 42.0	123.9	4,245	525,956
14. 17.0 x 43.5	122.3	4,401	538,242

* Average of three samples per specimen

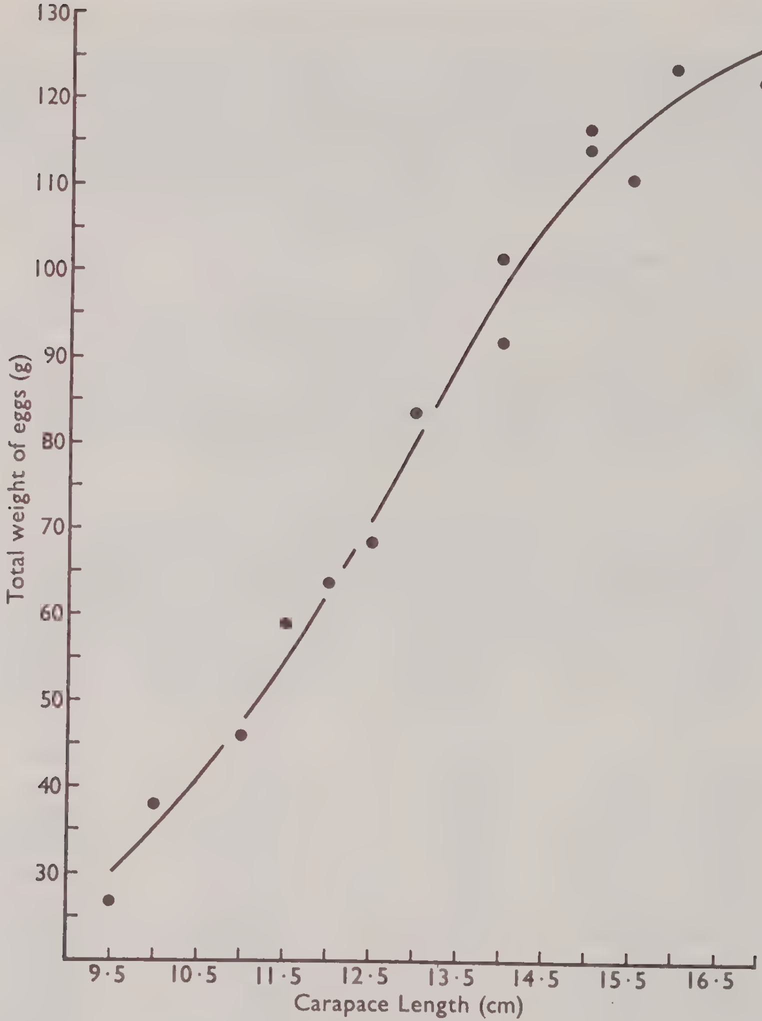

FIG. 1—Relation in *J. edwardsii* between the total weight of eggs carried and carapace length. The curve was fitted by eye.

Kensler (1967a) interpolated the results of Matthews (1962) and Heydorn (1965) and showed that the South African spiny lobster, *J. lalandii,* carried a greater total weight of eggs for a given carapace length than did the New Zealand species *J. verreauxi.* A comparison of fecundity results for similar sized specimens of *J. lalandii* (Matthews 1962) and *J. edwardsii* (based on Figs 1 and 3) is given in Table 2. It is evident that *J. lalandii* carries a greater total weight of eggs for a given carapace length than similar sized females of *J. edwardsii.* Table 3 shows comparative fecundity results for *J. edwardsii* (based on Figs 1 and 3) and *J. verreauxi* (Kensler 1967a). *J. edwardsii* is seen to carry

TABLE 2—Comparison of fecundity results for similar sized specimens of *J. lalandii* and *J. edwardsii*

Species	Carapace length (cm)	Total weight of eggs (g)	Number of eggs per 1 g sample	Total number of eggs
J. lalandii	9.5	54	5,278	285,000
	10.5	68	5,162	351,000
(Matthews,	11.5	84	4,976	418,000
1962)	12.5	97	5,041	489,000
J. edwardsii	9.5	30	3,833	115,000
	10.5	41	4,293	176,000
(Present	11.5	54	4,593	248,000
study)*	12.5	71	4,732	336,000

* Data interpolated from Figs 1 and 3

TABLE 3—Comparison of fecundity results for similar sized specimens of *J. edwardsii* and *J. verreauxi*

Species	Carapace length (cm)	Total weight of eggs (g)	Number of eggs per 1 g sample	Total number of eggs
J. edwardsii	15.5	117	4,333	507,000
	16.0	121	4,314	522,000
(Present	16.5	124	4,331	537,000
study)*	17.0	127	4,323	549,000
J. verreauxi	15.5	51	7,373	376,000
	16.0	69	6,971	481,000
(Kensler,	16.5	87	6,782	590,000
1967a)	17.0	103	6,757	696,000

* Data interpolated from Figs 1 and 3

a greater total weight of eggs than similar sized specimens of *J. verreauxi*. No data on weight of eggs per specimen were given by Hickman (1946) and Bradstock (1950), hence additional correlations are not possible.

AVERAGE NUMBER OF EGGS PER 1 GRAM SAMPLE

In *J. edwardsii* no relation was found between the average number of eggs per 1 g sample and increase in carapace length (Fig. 2). A low count of 3,541 eggs per 1 g sample was recorded from a 10.0 cm C.L. female, and a high count of 5,005 eggs from a 12.0 cm C.L. female (Table 1).

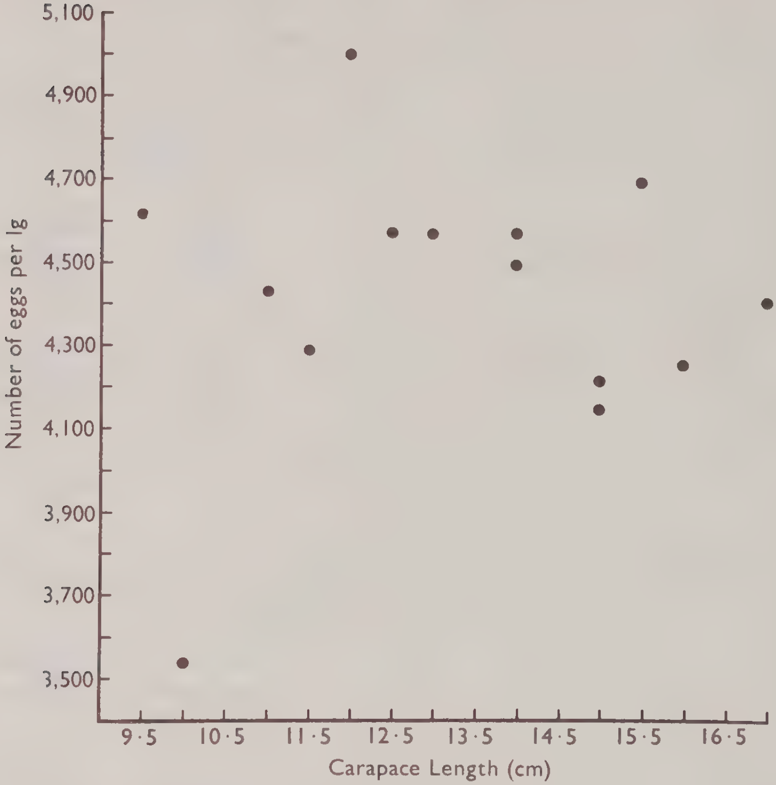

FIG. 2—Relation in *J. edwardsii* between the number of eggs per 1 g sample and carapace length.

Kensler (1967a) compared egg counts of several previously studied *Jasus* species and found a very much higher number of eggs per 1 g sample in the New Zealand spiny lobster *J. verreauxi*. The eggs of this species were apparently smaller than those of *J. novaehollandiae* from Tasmania (Hickman 1946), *J. edwardsii* from the Wellington region (Bradstock 1950), and *J. lalandii* from South African waters (Matthews 1962; Heydorn 1965). Additional, more detailed egg-count comparisons are now possible and are shown in Tables 2 and 3. Females of *J. lalandii* (Matthews 1962) and *J. verreauxi* (Kensler 1967a) are both noted to carry a greater number of eggs per 1 g sample than similar sized specimens of *J. edwardsii* (Tables 2 and 3). It appears, therefore, that the eggs of *J. edwardsii* (Chatham Islands) examined during the present study were larger than those of *J. lalandii* (South Africa) and *J. verreauxi* (northern New Zealand). Measurements of 100 individual preserved eggs from *J. edwardsii* (material from present study) and from *J. verreauxi* (material from Kensler's 1967a study) showed definitely that the eggs of the latter species were smaller in diameter. The 100 *J. verreauxi* eggs ranged in diameter from

0.500 mm to 0.677 mm, with an average diameter of 0.606 mm. The 100 *J. edwardsii* eggs ranged in diameter from 0.677 mm to 0.853 mm, with an average diameter of 0.748 mm. The *J. edwardsii* eggs were, therefore, about 20% larger than the *J. verreauxi* eggs. Larger egg size in *J. edwardsii* could also be accounted for by differences in egg stage development; the *J. edwardsii* eggs were well developed (with eye-spots), whereas the *J. verreauxi* eggs were newly laid (without eye-spots).

TOTAL NUMBER OF EGGS CARRIED

The total estimated number of eggs carried by *J. edwardsii* ranged from a low figure of 124,278 in a small female of 9.5 cm C.L., to a high figure of 538,242 in a large specimen of 17.0 cm C.L. (Table 1). The relation between the number of eggs carried and increase in carapace length is shown in Fig. 3. The rate of increase in fecundity (total egg production) is greater in smaller than in larger females, as is shown

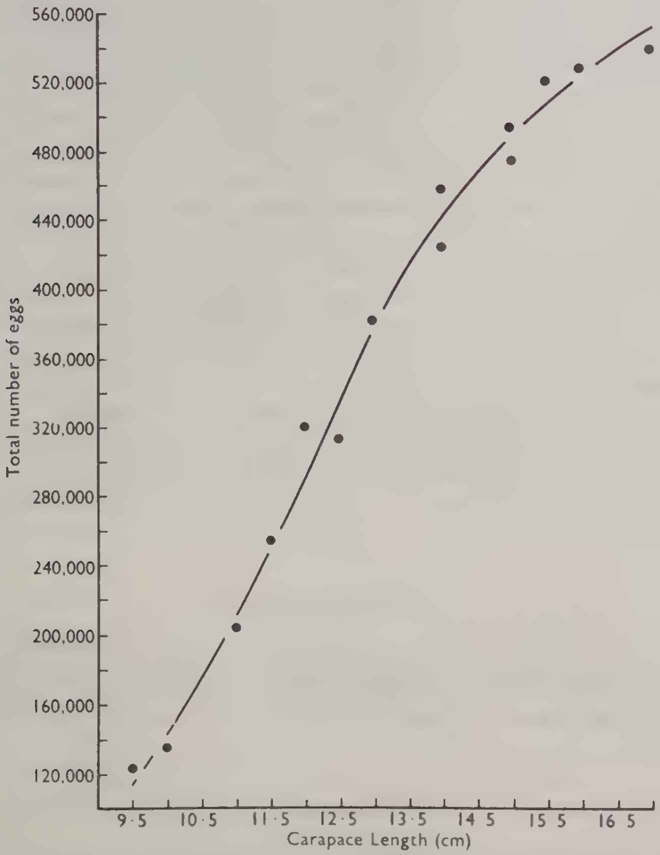

FIG. 3—Relation in *J. edwardsii* between the total number of eggs carried and carapace length. The curve was fitted by eye.

by the decrease in the slope of the curve (Fig. 3) with specimens above 14.5 cm C.L. Only a small variation was noted in the total number of eggs carried by *J. edwardsii* females within the same 5 mm carapace length group (Table 1). For example, the estimated total number of eggs carried by specimens No. 8 and 9 (i.e. 14.0 cm C.L.) differed by 35,578 eggs, or by about 8%; the estimated number carried by specimens No. 10 and 11 (15.0 cm C.L.) differed by only 18,919 eggs, or by about 4%. As mentioned earlier in this section, these slight differences could be due to individual variation in reproductive capacity and/or to differences in respective total lengths.

Because the *J. verreauxi* specimens examined were so much larger than other *Jasus* females previously studied, Kensler (1967a) was unable to make direct comparisons of their fecundity with that of other species of similar sizes. The smallest specimen was considerably larger than the largest female of the species used in each of the other egg-count studies.

Several comparisons of the total number of eggs carried by *J. edwardsii* (present study) and by similar sized specimens of *J. lalandii* (Matthews 1962) and *J. verreauxi* (Kensler 1967a) are now possible (Tables 2 and 3). The data presented in Tables 2 and 3 for *J. edwardsii* are based on interpolations of Figs 1 and 3. The results show that total egg production at any given carapace length is greater in *J. lalandii* than in *J. edwardsii* (Table 2). The comparative results given in Table 3 show that increase in fecundity with increase in carapace length is very much less in *J. edwardsii* than in *J. verreauxi* over the same size range. For example, a *J. edwardsii* female would produce only an additional 42,000 eggs with an increase in carapace length from 15.5 cm up to 17.0 cm, but with a similar increase in carapace length a *J. verreauxi* female would produce an additional 320,000 eggs. These results are explicable in terms of the age and size range of the two species examined. It has been pointed out by Kensler (1967a), and also found to hold true in this study (Fig. 3), that the rate of increase in fecundity is greater in smaller than in larger specimens. Therefore, being at the upper end of their size range (Fig. 3) females of *J. edwardsii* would be expected to carry fewer eggs for a given carapace length than similar sized females of *J. verreauxi*, at the lower end of their size range (Kensler 1967a, Fig. 5).

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9

The Nutrition of Pinnipeds

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INTRODUCTION

If we had to describe the extent of our knowledge of the nutritional requirements of seals in just three words we could probably best do so by saying "they eat fish." It is close to the truth that our knowledge does not go far beyond this simple statement. In this chapter I have attempted to review some of what is known and to point out the main gaps in our knowledge of this subject. Three general sources of information were used: (1) a review of the literature on the food of wild pinnipeds; (2) replies from 34 zoos and aquariums around the world to a questionnaire on feeding practices for captive pinnipeds; and (3) my own experience in developing a formula for newborn northern fur seals. These sources are augmented by references to the technology of seafood preservation and biochemical considerations related to vitamin requirements and electrolyte balance.

I thank the 34 zoos and aquariums that took part in the survey of pinniped feeding practices. Their contribution to this chapter is an important

one. I also thank V. B. Scheffer, Jane Church, and Ethel Todd for their editorial assistance, and Sharon Billings, Clifford Fiscus, and Hiro Kajimura for their help with library research.

A REVIEW OF THE LITERATURE ON THE FOOD OF WILD PINNIPEDS

The natural food of pinnipeds is determined mainly by an examination of the stomach contents. Other methods are observing actual feeding and examining feces or vomitus. Sometimes ecological and anatomical features constitute circumstantial evidence for feeding on certain kinds of food. Each species of pinniped is considered here in the same order and classification used by Scheffer and Rice (1963) in their list of the marine mammals of the world. Common names of fishes are used wherever possible. The main authority for these names is "A List of Common and Scientific Names of Fishes from the United States and Canada," Special Publication No. 2 (1960), of the American Fisheries Society.

Family Otariidae (seals with external ears)

Subfamily Otariinae (Sea Lions)

Otaria byronia (South American sea lion). Hamilton (1933, 1934) reported that adults eat squid, spider crab, medusae, birds, and fish (not identified), and that pups eat sea squirts and small crustaceans.

Eumetopias jubatus (Steller sea lion). The stomachs of 4 sea lions off California and Oregon contained flatfish and rockfish; 18 in Alaskan waters contained capelin, sand lance, rockfish, sculpins, and flatfish, and one contained salmon (Fiscus and Baines, 1966). Lucas (1899), who examined two stomachs from the Pribilof Islands, found fragments of the common crab of the Pribilofs and bones of sculpins. Wilke and Kenyon (1952), who examined two stomachs from St. Paul Island, Alaska, found sand lance, starry flounder, and sculpin in one, and halibut, flounder, cod, and pollock in the other. The weights of the contents were 4.5 and 9.0 kg, respectively. The weight of the stomach contents of a Steller sea lion taken off California was 16 kg (Bonnot, 1928). Examination of 114 stomachs from the Shumagin Islands, Alaska, revealed that fish made up 27 percent of the total volume of food (Mathisen et al., 1962). Most were smelts, rockfish, greenling, and sculpins; lampreys, salmon, and sand lance were incidental. Invertebrate food included squid and octopus (about 35 percent of the total volume) and common bivalves (near 20 percent); about 8 percent of the contents were shrimp and crabs. Nesterov (1964) reported that "Cephalopoda hold a prominent place in the nutrition of the sea lion" of the Commander Islands, USSR. Sea lions of the Kuril Islands, USSR, feed on Atka mackerel, sand lance, rockfish, whiting, squid, and octopus (Panina, 1966). Sea lions from Canadian waters (Pike, 1958) contained herring, rockfish, squid, octopus, skate, hake, salmon, halibut, and blackcod.

Zalophus californianus (California sea lion). References to the food habits of wild California sea lions are surprisingly few considering the large numbers and availability of these animals. Bonnot (1928) reported: "Of the 13 California sea lions whose stomachs contained food, 5 had eaten fish and 11 had eaten squid. The quantity of fish was inconsiderable, 17 small fishes being the maximum, while the remains of 100 to 300 squid were found in each of 5 stomachs." Of 24 stomachs from Monterey Bay and south along the coastline for 40 km, 18 contained squid, 3 contained octopus, and 4 were empty (Dyche, 1903). One stomach contained the remains of a 9 to 20 kg giant squid. Fiscus and Baines (1966) collected stomachs that contained hake, squid, and anchovies. Scheffer and Neff (1948) found herring and squid.

Neophoca cinerea (Australian sea lion; white-capped sea lion). I found no reference to the food of this species.

Neophoca hookeri (New Zealand sea lion). Csordas (1963) noted that sea lions on Macquarie Island feed on *Eudyptes* penguins but did not report other forms of food.

Subfamily Arctocephalinae (Fur Seals)

Arctocephalus australis (South American fur seal). I found no reference to the food of this species.

Arctocephalus doriferus (Australian fur seal). The stomachs of 138 of 246 seals from the Victoria coast contained food. The crayfish, *Jasus lalandii,* was a major food; other crustaceans, and squid and fish, including barracouta, were also important (McNally and Lynch, 1954). Lewis (1929) estimated that *A. doriferus* must eat hundreds of thousands of barracouta, judging from the great amount of barracouta bones lying on the rookeries; but only 12 of 57 fur seals killed on the rocks contained food, consisting mainly of barracouta and squid. Gurnets, crayfish, parrotfish, and "salmon-trout" were incidental.

Arctocephalus forsteri (New Zealand fur seal). Stomachs of 70 fur seals from Kaikoura Peninsula, Banks Peninsula, Otago Peninsula, Nugget Point, and Bench Island, New Zealand, contained 91 percent (by volume) barracouta, octopus, and squid. The largest amount in one stomach was contributed by the remains of four octopi weighing a total of 7 kg. The original weight of the octopi was probably about 10 kg each. The average weight of food taken in a meal was 4 to 5 kg (Street, 1964).

Arctocephalus philippii (Guadalupe fur seal). I found no references to the food habits of these species.

Arctocephalus pusillus (South African fur seal). From 1954 to 1956 the Division of Fisheries, Department of Commerce and Industries for the Union of South Africa, collected 245 stomachs at sea, of which 135 contained food. By frequency of occurrence, the contents were fish, 79 percent; cephalopods, 53 percent; and crustaceans, 19 percent. By volume the contents were fish, 67 percent; cephalopods, 21 percent; and crustaceans, 2 percent. Eighty percent of the fish were pilchards and maasbanker. Altogether, 24 species of fish were identified (Rand, 1959).

Arctocephalus tropicalis (Kerguelen fur seal). I found no reference to the food habits of this species.

Callorhinus ursinus (Northern fur seal). To 1966, 70 species of food items have been identified from fur seals of the eastern Pacific Ocean. In Alaskan waters the leading food species in 1958 and 1960 (1,248 stomachs with food) were herring, capelin, pollock, and sand lance, and in 1963 and 1964 (1,185 stomachs with food), they were squid, herring, capelin, pollock, and deep sea smelt (Anonymous, in press). The prominent food item in the Sea of Japan and the Okhotsk Sea was pollock; in the Okhotsk Sea the diet of nearly 50 percent pollock in July and August changed to mostly squid and Atka mackerel in September and October (Anonymous, 1965). Since 1958 the stomachs of 3,633 fur seals collected in California waters have been examined by the Marine Mammal Biological Laboratory, Bureau of Commercial Fisheries, U.S. Fish and Wildlife Service. The major foods were anchovy, hake, squid, and saury; squid predominated in 1958 and 1961; anchovy in 1959 and 1966; and hake in 1964 and 1965 (Fiscus and

Kajimura, 1967). Spaulding (1964) reported that the major food items in 2,113 stomachs collected off the coast of British Columbia were herring and squid, which together made up two-thirds of the total intake. Lamprey and salmon composed 7 percent each, and rockfish, sand lance, sablefish, birds, and stickleback contributed about equally to the remainder. The maximum amount found in the stomach of any one fur seal was equal to 10 percent of the seal's body weight. The average daily intake was 6 percent of the animal's body weight.

Family Odobenidae

Odobenus rosmarus (Walrus). Brooks (1952, 1954) studied the food of the Pacific walrus from the Bering Strait and in the Point Barrow area, Alaska. He recovered the following invertebrates from walrus taken during May and June in 1952 and 1953: Mollusca, *Mya truncata, Clinocardium nuttalli, Astarte* sp., *Macoma calcarea, Neptunea* sp.; Echinodermata, *Malpodia arctica*; Annelida, *Nephtys* sp.; Sipunculoidia, one unidentified genus; Priapuloidea, *Priapulus caudatus.* The full stomach of one bull weighed 50 kg; the food included 23 kg of siphons of *Mya truncata* and 16 kg of the feet of *Clinocardium nuttalli.*

Family Phocidae

Subfamily Phocinae

Phoca vitulina (Harbor seal). Fisher (1952) examined 50 stomachs of seals collected in British Columbia from September 1945 to November 1946. In the 20 stomachs that contained food, rockfish, octopi, and salmon were most prevalent. Also present were herring, shrimp, small crabs, and lamprey. Imler and Sarber (1947) found that the stomach contents of 67 seals from the Copper River delta, Alaska, consisted almost entirely of eulachon (the seals were taken during the eulachon run). Stomachs of 99 harbor seals from southeast Alaska contained mostly codfish; herring and flounder ranked next, and shrimp were eaten during July and August. Of 11 stomachs of harbor seals from Amchitka Island, Alaska, Kenyon (1965) found Atka mackerel in 8 and octopus in 4. One stomach contained 72 freshly eaten whole Akta mackerel that were 15 to 20 cm long and weighed up to 50 g. Wilke (1957) found that octopus was the most frequently taken food of seven seals at Amchitka Island. T. Scheffer and Sperry (1931) examined 100 stomachs of seals collected in Puget Sound between December 1927 and August 1930. The general distribution of food by volume was 93.6 percent fish, 5.8 percent molluscs, and 0.6 percent crustaceans. The chief species of fish, in order of frequency of occurrence, were flounders, Pacific herring, tomcod, hake, sculpins, pollock, shiners, cod, and rockfish.[1] Salmon were found in two stomachs. Squid were eaten in winter and octopi in summer. The major foods of 126 harbor seals from the coast of British Columbia were salmon, octopus, squid, herring, and rockfish, in that order (Spaulding, 1964). Twenty-nine of the seals were taken near creeks where salmon were spawning.

Pusa hispida (Ringed seal). Stomach contents of 47 ringed seals from Baffin Island waters showed that they had fed primarily on the pelagic amphipod *Themisto libellula* and to some extent on the schizopod *Mysis oculata* (Dunbar, 1941). McLaren (1958) reported that the ringed seal eats a wide variety of planktonic, nektonic, and benthonic food species; 72 species were identified from 152 stomachs.

Pusa sibirica (Baikal seal). At least one published reference in Russian is available (Anonymous, 1962).

Pusa caspica (Caspian seal). I found no references to the food of this species.

Halichoerus grypus (Gray seal). Rae (1960) cited the following references and foods: J. G. Millais (1906) - cod, saithe, pollock, ling, conger eel, "toadfish," "lumpfish," salmon, "seatrout," and halibut; G. A. Steven (1934) - herring and cuttlefish; F. F. Darling (1944, 1947, 1952) - saithe, lythe, conger eel, salmon, flatfish, and crustaceans; E. Hardy (1953) - cod and flounder; and R. M. Lockley (1954) - herring, mackerel, skate, ray, dogfish, conger eel, mussels.

Fisher and Mackenzie (1955) found food in 17 of 44 stomachs of gray seals collected from 1950 to 1954. By frequency of occurrence, cod, herring, salmon, hake, flatfish, shrimp, and flounder were about equally represented. Squid and dogfish were also present.

Histriophoca fasciata (Ribbon seal). According to Arseniev (1941) the ribbon seal feeds predominantly on deepwater fishes (mainly pollock) and cephalopods in the spring near Sakhalin Island, USSR.

Pagophilus groenlandicus (Harp seal). Fisher and Mackenzie (1955) examined stomachs of 81 harp seals from the Magdalen Islands, Canada.

Seventy-five contained herring; 13 contained flatfish. Also present were witch, plaice, and shrimp.

Erignathus barbatus (Bearded seal). Johnson et al. (1966) examined stomachs from 164 bearded seals collected near Point Hope, Alaska, from mid-November 1960 to mid-June 1961 and 29 stomachs collected near Kivalina in February, April, and June 1960. The percentages of the total volume contributed by major food species by month were: November - shrimp, 60; January - shrimp, 85; February - shrimp, 52, arctic cod, 24; March - hermit crabs, 56, shrimp, 25; April - shrimp, 51, crabs, 14; May - shrimp, 27, crabs, 24, unidentified decapods, 23; June - clams, 38, crabs, 24, and shrimp, 13. One published reference in Russian is also available (Kosygin, 1966).

Monachus monachus (Mediterranean monk seal). I found no references to the food of this species.

Monachus tropicalis (Caribbean monk seal). I found no references to the food of this species.

Monachus schauinslandi (Hawaiian monk seal). Rice (1964) examined two stomachs and two regurgitations and found octopi, moray eels, conger eels, flatfish, puffers, and goatfish.

Lobodon carcinophagus (Crabeater seal). Bertram (1940) reported that the normal diet of crabeater seals is exclusively euphausiids.

Ommatophoca rossi (Ross seal). A female Ross seal stomach contained a cuttlefish and two cuttlefish beaks, several large euphausiids, and a whiting-like fish (Brown, 1915). King (1964) gave the diet as cephalopods, krill, and fish.

Hydrurga leptonyx (Leopard seal). Hamilton (1939) reviewed the reports of five authors on the food of the leopard seal and examined 15 stomachs himself (total, 32 stomachs). In order of frequency of occurrence, they contained penguin, carrion, seal, fish, crustaceans, whale, and *Pelecanoides* (diving petrel).

Leptonychotes weddelli (Weddell seal). Various species of nototheniids, the most abundant antarctic fish, are the main food (Bertram, 1940). Adults feed about equally on fish and cephalopods off the west coast of Graham Land; the proportion of cephalopods is lower in the Ross Sea. The fish eaten are usually 22 to 45 cm long. The stomach of an adult when full holds about 8 kg of food. The transitional diet for pups is largely crustaceans, as for the harp seal (Bertram, 1940). Ray (1966) has observed 24 kg antarctic cod brought to the surface and eaten.

Cystophora cristata (Hooded seal). Hooded seals "are said to eat octopus, squid, rosefish, herring, capelin, cod, shrimp, mussels, and starfish" (King, 1964).

Mirounga leonina (Southern elephant seal). Of 139 stomachs examined by Laws (1956), only 6 contained freshly eaten food and none were full; 23 contained cephalopod remains, 6 contained fish remains only, and 3 contained both fish remains and cephalopod beaks. The fish remains were predominantly species of *Notothenia.*

Mirounga angustirostris (Northern elephant seal). According to King (1964) the diet is fish, squid, ratfish, skates, and sharks.

A SURVEY OF FEEDING PRACTICES FOR PINNIPEDS IN ZOOS AND AQUARIUMS

Questionnaires on the feeding of pinnipeds were completed by 34 curators in Australia, Austria, Belgium, Canada, England, Germany, Italy, Japan, New Zealand, South Africa, the USSR, and the United States (California, Florida, Hawaii, Illinois, New York, Oklahoma, Pennsylvania, Texas, Utah, Washington, and the District of Columbia). Some institutions keeping pinnipeds were probably left out of the survey because there was no practical way of knowing which institutions kept pinnipeds. About one-third of the 64 institutions contacted did not respond; some that replied did not have pinnipeds in their care.

Fifteen of the 31 recognized species of pinnipeds (Scheffer and Rice, 1963) were reported on. The species and the foods fed to them are listed below. The institutions are usually identified by a number in the text, and by name and number in Table 1.

Species of Pinnipeds and Food Fed to Them in Captivity

Otaria byronia (South American sea lion). Two institutions (2, 3) reported that they were feeding South American sea lions. One (2) feeds mostly cod and sometimes Atlantic herring; the other feeds only whiting.

Table 1

34 ZOOS AND AQUARIUMS THAT PARTICIPATED IN THE SURVEY OF PINNIPED FEEDING PRACTICES

Australia

1. Taronga Zoological Park Trust
Zoological Gardens & Aquarium
Mosman, Sydney, N.S.W.
Australia

Austria

2. Aquarium, Schönbrunn Zoo
Tiergarten Schönbrunn
Vienna XIII, Austria

Belgium

3. Société Royale de Zoologie d'Anvers
Antwerpen
Koningin Astridplein 26, Belgium

Canada

4. Calgary Aquarium
9th Avenue & 15th Street S.E.
Calgary, Alberta, Canada

England

5. Zoological Society of London
Regent's Park
London N.W. 1, Great Britain

Germany

6. Aktien Verein des Zoologischen
Gartens zu Berlin
1 Berlin 12
Hardenbergplatz 8, Germany

Italy

7. Giardino Zoologico e Museo
di Zoologia
Commune de Roma
Viale Giardino 20
Rome, Italy

Japan

8. Enoshima Aquarium
2938 Katase
Fujisawa, Kanagawa Pref.
Honshu, Japan

9. Ueno Zoological Garden
Ueno Park
Daito-ku, Tokyo, Japan

New Zealand

10. Auckland Zoological Park
Grey Lynn
Auckland W2, New Zealand

South Africa

11. East London Aquarium
Esplanade
East London, South Africa

12. Johannesburg Zoological Gardens
Jan Smuts Avenue
Johannesburg, South Africa

USSR

13. Moskovskii Zoologicheskii Park
Moskva G-242
Bolshaya Groozinckaya U1, D No 1
USSR

United States

14. Biological Sonar Laboratory
Stanford Research Institute
Menlo Park, California 94025

15. Griffith Park Zoo & Los Angeles Zoo
Room 305, City Hall
Los Angeles, California 90012

16. Sea World
1720 South Shores Road
San Diego, California 92109

Table 1 (concluded)

United States (continued)

17. Shipwreck Aquarium
P. O. Box 322
Eureka, California 95501

18. Steinhart Aquarium
California Academy of Sciences
Golden Gate Park
San Francisco, California 94118

19. National Zoological Park
Smithsonian Institution
Washington, D.C. 20009

20. Aquatarium
Marine Attractions Ltd.
St. Petersburg Beach, Florida 33736

21. Gulfarium
Box 29
Fort Walton Beach, Florida 32548

22. Marineland of Florida
Route 1, Box 122
St. Augustine, Florida 32084

23. Honolulu Zoo
Waikiki Beach
Kapiolani Park
Honolulu, Hawaii 96815

24. Sea Life Park
Makapuu Point
Waimanalo
Oahu, Hawaii 96795

25. Waikiki Aquarium
2777 Kalakaua Avenue
Honolulu, Hawaii 96815

26. Lincoln Park Zoological Gardens
100 West Webster Avenue
Chicago, Illinois 60614

27. New York Aquarium
New York Zoological Society
Boardwalk at W. 8th Street
Coney Island
Brooklyn, New York 11224

28. Oklahoma City Zoo
Route 1, Box 478
Oklahoma City, Oklahoma 73111

29. Aquarama Theatre of the Sea
3300 South Broad Street
Philadelphia, Pennsylvania 19145

30. Dallas Aquarium
Fair Park
621 E. Clarendon Drive
Dallas, Texas 75203

31. Fort Worth Zoological Park &
James R. Record Aquarium
2727 Zoological Park Drive
Fort Worth, Texas 76110

32. Hogle Zoological Gardens
P. O. Box 2337
2600 Sunnyside Avenue
Salt Lake City, Utah 84110

33. Westport Aquarium
Harbor Street
Westport, Washington 98595

34. Woodland Park Zoological Garden
5400 Phinney Avenue North
Seattle, Washington 98103

Eumetopias jubatus (Steller sea lion). Five institutions (16, 1, 14, 8, and 9) reported that they were feeding Steller sea lions. The principal foods fed were: 16 - Spanish mackerel, smelt, squid; 1 - striped mullet; 14 - Pacific herring, Pacific mackerel, Spanish mackerel, whitebait smelt, American smelt; 8 - mackerel; 9 - mackerel.

Zalophus californianus (California sea lion). Twenty-five respondents hold California sea lions. The most widely fed foods, in order of greatest frequency, are herring, mackerel, smelt, and squid.

Neophoca cinerea (Australian sea lion; white-capped sea lion). Only one respondent holds this species--Taronga Zoological Park, Sydney, Australia. The one Australian sea lion is fed striped mullet primarily but also fantail mullet, mackerel, "Cowanyoung," and Pacific bonito.

Arctocephalus pusillus (South African fur seal). South African fur seals are kept by five institutions and are fed as follows: 11 - *Johnius hololepidotus, Trachurus trachurus* (jack), *Merluccius capensis* (hake); 6 - herring; 2 - cod, Atlantic herring; 3 - whiting, herring; 12 - South African hake.

Callorhinus ursinus (Northern fur seal). Six institutions keep northern fur seals: 27 - herring, mackerel; 33 - squid, herring, cod, anchovy, smelt; 4 - herring; 34 - herring, squid and sole (occasionally); 14 - herring, Spanish mackerel, whitebait smelt, mud suckers (live for weaning); 8 - mackerel.

Odobenus rosmarus (Walrus). The New York Aquarium feeds its walrus surf clams (*Spisula solidissima*). The Moscow Zoo feeds its walruses *Caspiolosa* sp., *Clupea* sp. (herring), *Merluccius* sp., *Coregonus albula, Clupeonella* sp., and *Osmerus eperlanus* (smelt).

Phoca vitulina (Harbor seal). The food of captive harbor seals was reported by 18 institutions. The most widely fed foods, in order of greatest frequency, were herring, mackerel, smelt, and squid.

Pusa hispida (Ringed seal). Two respondents are feeding ringed seals: 27 - herring, mackerel; 6 - cod, herring.

Pusa sibirica (Baikal seal). The Baikal seal at the Antwerp Zoo is fed sprat. No other Baikal seals in captivity were reported.

Halichoerus grypus (Gray seal). Three respondents are feeding gray seals: 27 - herring, mackerel; 6 - herring; 5 - whiting, herring.

Monachus schauinslandi (Hawaiian monk seal). Two respondents are feeding Hawaiian monk seals: 24 - mackerel, smelt, moray eels, squid, reef fish, tuna; 25 - herring, smelt, akule, skipjack tuna.

Hydrurga leptonyx (Leopard seal). The leopard seal at Taronga Zoo, Sydney, Australia, is fed striped mullet primarily but also fantail mullet, mackerel, "Cowanyoung," and Pacific bonito.

Mirounga leonina (Southern elephant seal). Five respondents are feeding southern elephant seals: 7 - mackerel, sardines, *Octopus* and *Ommastrephes sagittatus* (occasionally); 8 - mackerel; 9 - mackerel; 6 - herring; 3 - whiting.

Mirounga angustirostris (Northern elephant seal). Three respondents are feeding northern elephant seals: 15 - mackerel; 16 - mackerel, smelt, squid; 14 - mackerel, herring.

Sources of Food Fed to Captive Pinnipeds

Twenty-three institutions buy frozen fish from local wholesale dealers and eight buy from distant dealers. Five institutions buy fresh fish locally and one does its own collecting. Two other sources given were city market place and government fish market.

Preservation and Storage of Seafood

Most (29) of the respondents preserve and store their food for pinnipeds by freezing. One institution feeds live fish and one uses refrigerated brine. Five institutions use refrigeration but not necessarily freezing, and five feed some fresh fish in addition to frozen fish.

Packaging

Several methods of packaging were given--plastic, paper, wooden and cardboard box, plastic bag and cardboard box; polyethylene bags; wax-lined paper bags; waxed cardboard cartons; glazed, frozen, and loose in aluminum trays. Most institutions use plain cardboard or wooden boxes.

Storage Temperature

The temperature ranges (°C) and number of institutions using them are as follows: -29 to -23, 8; -22 to -12, 10; -11 to -7, 5; -6 to -1, 9; not given, 2.

Maximum Storage Time before Discarding

The time ranges and number of institutions using them are as follows: 2 to 7 days, 8; 14 to 30 days, 6; 4 to 6 months, 6; 9 to 11 months, 3; 11 to 12 months, 8; not given, 3.

Preparation of Frozen Seafood for Feeding

Thawing

The methods of thawing and number of institutions using them are as follows: at room temperature, 4; at ambient temperature, 2; at 2° to 5°C, 4; in standing fresh water, 6; in running fresh water, 12; in standing seawater, 2; in running seawater, 4; at ambient temperature overnight, then finished in fresh water, 2; not given, 3.

Trimming

Some trimming is done by 10 respondents; the rest do no trimming. Examples of trimming are removing the heads and tails from sablefish; removing various parts from cut fish; removing tails, fins, and viscera from fish that are headless when received; removing heads, tails, and most viscera; and removing spines and fins from butterfish.

Lubrication

One institution rolls fish in codliver oil and vitamin mix for newly weaned seal pups; another dips the fish in a special lubricative solution of seawater, codliver oil, or seal oil. None of the others reported any kind of routine lubrication.

Weighing

Thirteen institutions weigh the food before feeding and 10 do not. The 11 others estimate the weight, usually from a weighed larger amount.

Form and Size of Food

Of the 34 institutions, 25 feed whole fish. The fish are generally 10 to 20 cm long. Eleven institutions feed small (5 cm) chunks, and five feed large chunks (5 by 15 cm). Some fish are received without viscera.

Methods of Feeding

Amount

Almost half (16) of the institutions feed an amount per day equal to 6 to 10 percent of the animal's body weight. Generally the amount fed to larger animals (elephant seals and Steller sea lions) is much lower (1.6 to 3.0 percent of the body weight). At some institutions the seals are fed by visitors, and the keepers supplement this food with a better quality fish. Under this arrangement some seals are fed almost constantly. Seals are sometimes fed more in winter than in summer. Also, the amount fed is regulated by the apparent appetites of the seals.

Frequency

Most (20) of the respondents feed twice a day, four feed once a day, and four feed three times a day. Some seals are fed intermittently throughout the day, usually by the public; and some institutions feed four to six times a day.

Regulating Individual Intake

All but six institutions regulate individual intake in some way: hand feeding, luring the more aggressive eaters to one side, feeding an excess, and extra feeding while individually caged are some of the methods. Visitors reportedly make a special attempt to get food to the weaker, less aggressive individuals.

Nutritional Supplements

Vitamins

The feeding of vitamins was reported by 28 (81 percent) of the institutions; the other six do not feed vitamins. With a few exceptions all respondents feeding vitamins reported giving some kind of multiple vitamin pill or capsule; 25 brands were listed. Some vitamins were given instead of, or in addition to, the multivitamin; the vitamins mentioned were A, D, B_1, B_{12}, and C. Surprisingly, only one institution reported giving codliver oil.

The usual dosage for seals and sea lions was one multivitamin pill or capsule per day. One or two capsules a week and two pills per day were also reported.

The dosages of different vitamins were as follows: vitamin A, 10,000 to 50,000 units/animal/day and 50,000 to 100,000 units/week; vitamin D, 400 to 1,000 units/day; vitamin C, 50 to 500 mg/day; B_1, 7.5 to 100 mg/animal/day; and B_{12}, 3 μg/animal/day.

The reported dosage for elephant seals was: One institution gives 10 multivitamin capsules, 100,000 units of vitamin A, and 6,000 units of vitamin C per day to a 909 kg (1 ton) elephant seal. Two institutions give two or three multivitamin capsules per day to such an animal.

The New York Aquarium gives the following daily vitamin doses to the walrus: A, 250,000 units; D, 10,000 units; B_1, 100 mg; B_2, 50 mg; B_6, 10 mg; B_{12}, 50 μg; C, 1,500 mg; niacinamide, 1,000 mg.

Route of Administration

Two institutions give vitamins by intramuscular injection in addition to the oral route used by all the other respondents.

Minerals

Most institutions do not supplement minerals except to the extent that minerals are present in multivitamin preparations, but seven respondents reported feeding such minerals as calcium, iron, manganese, potassium, zinc, magnesium, sodium chloride, USP Salt XIV, hematinics, and "Nova kelp."

Observations of Feeding Behavior

Gorging, Choking, and Vomiting

Gorging, observed by 11 of the respondents, was attributed to a number of reasons. It may be seen in newly caught seals, or after a change in diet. Some keepers reported a tendency of seals to overeat when fed certain kinds of fish, and they believe animals would gorge more often if given the chance. South African fur seals and California sea lions are reportedly very greedy eaters. Animals may regurgitate the excess or fast for a day or two. One California sea lion makes gorging serve a useful purpose by regurgitating in the deepest part of the pool and eating the cached food later when no more surface food is available. This is the only reported example of food storage by a marine mammal.

Choking has been observed by 15 of the respondents. Some of the reasons for choking were: swallowing fish or chunks of food that were too large; gulping food or swallowing fish tail first; swallowing an unexpected mouthful of water (as when swallowing a fish and at the same time swimming after another one); and attempting to swallow foreign objects such as sticks, balls, or plastic bags.

Vomiting was noted by 15 institutions. Some observers feel that the vomiting of fish skeletons and squid beaks is a normal physiological process. Seals have also been seen regurgitating foreign objects. Some South American fur seals vomited after eating leaves, and a walrus vomited rocks and oxidized coins. Overeating or eating spoiled fish is said to cause vomiting. Roundworms are thought to be another cause.

Elimination

Twenty-two institutions answered "yes" and 10 answered "no" when asked if they could routinely examine the character of the feces and urine of pinnipeds. Some are able to observe feces but not urine.

Fasting

Twenty-two institutions observed fasting among their pinnipeds. To some, fasting is a sign of illness and they call their veterinarian immediately. New animals, breeding animals, and animals in moult, however, appear to fast regularly for periods of a few days to one or two weeks. (The breeding fur seal bull may fast in the wild for more than 60 days.) At times fasting is attributed to a monotonous diet; a change stimulates the animals to resume eating. Some pinnipeds have been observed to eat less in summer than in other seasons. Some animals fast for no apparent reason.

Convulsions, Food Poisoning, and Unusual Reactions Associated with Feeding

Convulsions were noted by nine respondents. The consensus of these observers is that convulsions are always either a sequel to illness of some kind (particularly heat prostration) or a prelude to death. Illnesses such as Chastek's paralysis, pneumonia, filariasis, and hypovitaminosis are thought to be the more usual causes, but some believe that simple indigestion from overeating can precipitate convulsions, particularly in the greedy eaters.

Food poisoning from a buildup of toxin from microorganisms is virtually unreported in captivity, but two probable instances were reported in the present survey--both attributed to spoiled fish. One example reported by Bullier (1935) was of illness caused by herring preserved chemically for salmon bait.

Unusual reactions or (more aptly) idiosyncrasies associated with feeding were reported by only seven respondents. An example is the refusal of fresh herring by an animal accustomed to frozen herring. Several days may be required to change a diet from one kind of fish to another. Well-fed seals resist changes in diet. Sometimes animals tire of certain species of fish; offering a variety then stimulates the appetite. New animals (especially very young animals) sometimes reject fish heads and tails, and some refuse fish that are too large or have hard scales. One institution reports that very fat herring are rejected.

Ingestion of Rocks

Although only three institutions make rocks available to their pinnipeds to swallow if they wish, eight institutions reported the accidental introduction of rocks which were possibly, and at times known to be, swallowed by seals. The swallowing of rocks and pebbles by seals can be deliberate or accidental. Usually, curators believe that seals which swallow rocks tolerate them without ill effects. At the Antwerp Zoo the South American and California sea lions, elephant seals, and harbor seals eat considerable amounts of sand and pebbles; the Baikal seal likes to search the bottom much like a duck.

THEORETICAL NUTRITIONAL REQUIREMENTS OF CAPTIVE PINNIPEDS

Preference of Wild Pinnipeds for Certain Food Species

How important is it to feed captive pinnipeds what they are likely to eat in the wild? The answer depends on whether natural feeding is regulated by circumstance or by uncompromising nutritional requirements. With few exceptions, natural feeding appears to be regulated mostly by circumstance. Animals tend to feed on species that are most abundant, within their geographical range, and most easily caught and devoured.

The Nutritive Value of Fish

Fish is equal to meat and poultry as a source of animal protein, vitamins, and inorganic components. Fish protein is high in essential amino acids. Up to one-third of the oil in fish is highly unsaturated, with molecules of fatty acids having up to six double bonds (Osterhaug et al., 1963). Captive pinnipeds given dead fish often show the effects of nutritional deficiencies, but the nutritional requirements of pinnipeds are satisfied by fish that are eaten alive. Apparently the characteristics that make whole fish a splendid food also make it subject to rapid deteriorative and other changes which either deprive the animal of nutrition or poison it.

Deteriorative Changes in Seafoods

Microbiological Changes

According to Liston et al. (1963) the external surfaces of all marine animals carry large numbers of bacteria, and in free-swimming fish, the numbers on the skin range from 10^2 to $10^6/\text{cm}^2$, and in the intestine, from very few in nonfeeding fish to $10^7/\text{g}$ in feeding fish.

> The internal tissues and organs of healthy fish and shellfish appear to be sterile. In general, the bacteria found on living fish are predominantly psychrophilic (growing significantly at 32°F), sea water loving (though not necessarily absolutely halophilic), aerobic, and attack proteinaceous materials more actively than carbohydrates. Genera of bacteria repeatedly found on fish include *Pseudomonas, Achromobacter, Vibrio, Flavobacterium, Corynebacterium, Alcaligenes, Photobacterium, Micrococcus, Mycoplana, Proteus, Bacillus,* and (in the intestine) *Clostridium.*

Rough handling that causes breaks in the skin allows penetration of the tissues by bacteria and hastens spoilage. Any laxity in temperature control causes accelerated bacterial growth and more rapid spoilage.

Chemical Changes

The changes in texture which occur in frozen fish during storage or in freeze-dehydration are ascribed to denaturation of the labile fish protein. Various side chains of proteins may also enter into other types of reactions. The disulfide bond (–S–S–) of cystine may be converted to sulfhydryl (–SH) or cysteine by reducing agents. The free amino groups of proteins are available for reactions with reducing sugars or with some of the products of oxidation of lipid material (Liston et al., 1963).

Fish oils hydrolyze to form free fatty acids, as occurs in other food lipids. Oxidation of the fatty acids, which gives rise to numerous carbonyl types of products, is the chief cause of rancidity in fish oils (Liston et al., 1963). The oil in the area of the fish known as the dark meat--such as occurs, for example, along the lateral line--oxidizes at far greater rates than oil in the light meat portions of the fish (Brown et al., 1957).

Freezing and Cold Storage of Seafoods

> The quality of frozen fishery products is influenced by many different considerations. Among the most important are composition of fish, prefreezing handling and treatment, method of freezing employed, and the environment to which the frozen product is subjected during storage and handling. Of principal concern is the temperature and humidity of the cold-storage area and the protective packaging or glazing (Slavin, 1963).

Fish with high oil content are more susceptible to oxidative changes than fish with low oil content. The relative suitability of different fish for freezing and cold storage is indicated in Table 2.

Partly spoiled fish have a much shorter frozen shelf life than fresh-frozen fish. Slavin (1963) found that the chilled storage age of whiting profoundly affects the quality of the frozen fish (see Table 3).

Temperature and time of storage are the most important factors influencing the quality of frozen seafood. Lean fish such as haddock or cod should be kept at -18°C or lower. Fatty fish such as mackerel, sea herring, or tuna should be stored at -30°C or lower (Slavin, 1963).

The storage life of frozen fish can be increased significantly by packaging, glazing, or both. Conventional waxed cartons, overwrapped with films containing polyethylene, waxed paper, cellophane, or combinations of these materials, are generally not suitable because they are not resistant to gas transmission and do not fit the product tightly. Pouches and bags made of polyester films coated with or laminated to polyethylene, cellophane, polyvinylidene chloride, or aluminum foil are satisfactory (Slavin, 1963).

The relative humidity is a comparison of the amount of moisture in the air, at a particular temperature, with the moisture which the air can theoretically hold. Frozen fishery products contain about 80 percent water and therefore have a relatively high moisture-vapor pressure. As the relative humidity of the storage environment is decreased, the moisture-vapor pressure of the air decreases proportionally, causing a greater difference between the moisture-vapor pressure of the fish and that of the surrounding air. Moisture then migrates from the product to the surrounding air until equilibrium is established. Slavin (1963) found that whole tuna stored at -18°C for 10-1/2 months at a relative humidity of 70 to 80 percent lost 20 times more weight than at a relative humidity of 90 to 95 percent.

Table 2

DEGREE OF SUITABILITY OF FISHERY PRODUCTS FOR FREEZING AND FROZEN STORAGE[a]

High (storage life of 7 to 12 months at 0°F)	Moderate (storage life of 5 to 9 months at 0°F)	Low (storage life of 4 to 6 months at 0°F)
Haddock	Ocean perch	Mackerel
Cod	Whiting	Tuna
Flounder	King, red, or coho salmon	Catfish
Hake	Lake herring	Sea herring
Shrimp	Red snapper	Spanish mackerel
Halibut	Smelt	Pacific sardines
King crab	Crawfish	Clams
Dungeness crab[b]	Rockfish	Chub
Pollock	Carp	Chum or keta salmon
Sea scallops	Buffalofish	Whale meat
Blue pike	Swordfish	
Yellow perch	Pacific oysters	
	Alewives	
	White bass	

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[a] After Slavin (1963). Data apply to products properly packaged.

[b] More recent studies show that, in general, Dungeness crab has a moderate storage life at 0°F. (Richard Nelson, Bureau of Commercial Fisheries, Technology Laboratory, Seattle, Washington, personnal communication).

Table 3
EFFECT OF CHILLED STORAGE AGE ON
SHELF LIFE OF FROZEN WHITING[a]

Period of Storage in Ice at 32°F	Shelf Life Stored at 0°F
(days)	(months)
0	12
2	12
4	6
7	2
9	0
11	0

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[a] After Slavin (1963).

Thawing and Trimming of Fish for Feeding

Both the flavor of fish and many of its nutritive components are soluble in water; therefore, thawing unwrapped fish in water is wasteful. Since the nutritional requirements of pinnipeds in the wild apparently depend on the consumption of whole live fish, as far as possible whole, fresh fish should be fed to captive pinnipeds.

Vitamin Supplements for Captive Pinnipeds

Most (81 percent) of the curators who responded to the questionnaire on this subject think it is necessary to feed a vitamin supplement to captive pinnipeds. No two institutions, however, fed the same formulation of multiple vitamins or the same dosage of individual vitamins. There apparently is considerable uncertainty about which vitamins to feed, how much, and how often, or whether to feed vitamins at all; 19 percent of the reporting institutions do not feed vitamin supplements. Do their animals fare any worse than those that get a vitamin supplement? Only controlled experimentation can give a definite answer. In my opinion, pinnipeds that are not fed a vitamin supplement but are fed a variety of seafoods that have been preserved in as fresh a state as possible will be healthier than pinnipeds fed vitamins and one species of seafood which has been improperly stored so that most of the nutritives have dissipated. Two possible exceptions involve vitamins E (tocopherol) and B_1 (thiamine).

Vitamin E (alpha-tocopherol)

Diets high in polyunsaturated fats require relatively high levels of vitamin E (Witting and Horwitt, 1964). Fish oils have a higher degree of polyunsaturation than any other natural oil; therefore, pinnipeds are subject to an increased requirement for vitamin E. This is apparently not a problem for pinnipeds in the wild. Theoretically, the problem for captive pinnipeds is proportional to the amount of chemical change allowed to take place in their food before it is fed to them. Deficiencies of vitamin E cause muscular dystrophy in calves and lambs, encephalomalacia in chicks, hock deformity in turkeys, impaired reproductivity in several species (Maynard and Loosli, 1956), and steatitis (yellow fat disease) in mink and swine that are fed raw fish (Runnels, 1954). Steatitis has also been reported in cats (Smith and Jones, 1961). To what extent any of these conditions occur in pinnipeds, wild or captive, is unknown. Steatitis in mink fed 85 percent fish scraps can be prevented by feeding 10 to 20 mg of vitamin E/mink/day (Jones, 1954). The amount required by pinnipeds is unknown.

Vitamin B_1 (thiamine)

> Some fur-bearing animals (foxes, mink, and ferrets) when fed continuously a ration containing certain frozen fish such as carp, Great Lakes herring, Atlantic herring, Pacific mackerel, mullet, northern pike, smelt, and suckers, display the following symptoms: anorexia, weakness, emaciation, diarrhea, and paralysis terminating in death. Because the symptoms of paralysis are so prominent, and because the disease was first recognized on the Chastek Fur Farm in Minnesota, the disease is usually referred to as Chastek paralysis (Runnels, 1954).

Chastek paralysis is caused by a deficiency of thiamine. The deficiency is brought about by an enzyme, thiaminase, which destroys thiamine and is found naturally in fresh fish (see also Hubbard, this book). In the past many thought there was little or no thiaminase activity in saltwater fish but this belief must have been based on inaccurate assay techniques. Deolalkai and

Sohonie (1957) found thiaminase activity in all of the saltwater fish they studied (16 species, including *Sardinella* and *Clupea*). They also found three optimum pH levels and hypothesized that saltwater fish have three different thiamine-destroying enzymes. The liver, kidney, spleen, and other viscera showed high activity for all three thiaminases. Some investigators have found that the skeleton, head, fins, and skin are the main sites of thiaminase activity (Green et al., 1941).

Rigdon and Drager (1955) reported on thiamine deficiency in three California sea lions fed fresh-frozen whiting at the rate of 5 lb/day. Two showed nerve degeneration and one showed cardiac lesions typical of beri beri in man. Such documented cases of thiamine deficiency in pinnipeds are difficult to find, yet most seal keepers are well aware of the potential hazards of thiaminase. No doubt the practice of feeding a vitamin supplement is aimed primarily at this potential hazard. Apparently it is not a hazard for wild pinnipeds which eat live seafoods. There may be a mechanism in fish after death, perhaps the release of a coenzyme, necessary to activate thiaminase. Another explanation is the possible synthesis of thiamine by the gut of the seal to offset thiaminase in the diet. Still another explanation might be that live fish contain a favorable balance of thiamine over thiaminase so there is a net gain of thiamine for the animal if it eats fish alive or in a reasonably fresh state before much thiamine has deteriorated.

Mink require 1.2 mg of thiamine per kg of basal diet for normal growth and fur development (Leoschke and Elvehjem, 1959). Swine require 1.1 mg/kg of feed (Maynard and Loosli, 1956). The daily thiamine requirement for pinnipeds is unknown.

Amount and Frequency of Feeding

Although captive pinnipeds, at least the smaller varieties, seem to get along nicely on a daily intake equal to 6 to 10 percent of their body weight, growing, pregnant, and lactating animals require more. Elephant seals and walrus can be maintained at a lower rate.

Feeding the total daily ration at one time can lead to problems of overeating. At least two feedings, and preferably three or four, will prevent most of these problems.

Ingestion of Rocks

Rand (1959) gave a thorough review of the many theories of why pinnipeds swallow rocks. Because rock ingestion is so widespread and rocks occur so frequently in the stomachs of collected animals, the possibility that it has some purpose associated with nutrition or some other physiological function cannot be discounted.

Accounts of rock ingestion by various pinnipeds in captivity were reported in an earlier section of this chapter. More numerous are reports of rock ingestion by wild pinnipeds. Fiscus and Baines (1966) found stones up to 12 cm in diameter in 16 of 32 Steller sea lion stomachs. Scheffer and Neff (1948) found rocks in three of four California sea lion stomachs; one contained 26 small rocks. Lewis (1929) reported finding pebbles or stones in many of 57 Australian fur seals killed on the Seal Rocks off the Victorian coast. Mathisen et al. (1962), Spaulding (1964), Nesterov (1964), and Panina (1966) all reported finding rocks in the stomachs of Steller sea lions. Stones up to 2 kg or more were found in as many as 64 percent of 114 animals (Mathisen et al., 1962). Rocks were swallowed even by young Steller sea lions that were still feeding on milk (Panina, 1966). Fifty percent of the stomachs of 20 northern fur seal pups, collected just before their fall migration, contained pebbles (Kajimura, 1968).

Research in Pinniped Nutrition

Vitamin Requirements

Controlled feeding experiments with young animals, both weaned and unweaned, are needed to determine what vitamins are necessary and at what levels. At present no institution is in a position to use animals for this purpose. All are simply doing their best to try to keep their animals alive and healthy. If a number of the zoological societies would pool their resources to sponsor appropriate research, the proper care and feeding of captive pinnipeds could become much more certain.

Electrolyte Balance

How to achieve proper electrolyte balance in captive pinnipeds in or out of seawater is a major problem to be solved. Many animals do well under a variety of feeding regimes and other conditions, but longevity of pinnipeds in captivity is not as great as it should be, nor is the rate of growth of some species.

Diet

It is difficult to maintain standards of quality and balance when the diet is made up of such a perishable and changeable foodstuff as raw fish, both fresh and frozen. A more stable and available supply of a food of standard quality would be a real boon to institutions that keep animals which require a seafood diet. Through technology, education, and management, we should be able to improve the present quality of pinniped diets. A possible food item in the future is a processed fish product such as might be made from whole fish meal, pressed into highly stable and nutritious chunks or sticks that many captive species would thrive on. The problems of rapid spoilage and vitamin degradation in fresh and inadequately packaged frozen fish would be eliminated.

ARTIFICIAL DIETS FOR NURSING PINNIPEDS

Northern Fur Seal *(Callorhinus ursinus)*

During the summers of 1963 through 1965 on St. Paul Island, Alaska, I developed a satisfactory diet for newborn northern fur seals (Keyes, 1964, 1965, 1966). A pup from the 1966 trials was the first otariid to be raised artificially from birth to over one year of age.[2] Further testing was done in 1967. The current formula for artificial fur seal milk is presented in Table 4 followed by an explanation of the theoretical and empirical bases.

Theoretical Basis for the Formula

The formula was based on analyses of fur seal milk (Ashworth et al., 1966).

Proteins

Several proteins with amino acid compositions similar to that of seal milk were tested. These included soy flour (which has been used as a food for human infants) and bovine casein and lactalbumin and their hydrolysates. During the first and second series of feeding trials (involving a total of 29 newborn fur seals), none of the formulas based on these proteins supported weight gains or kept newborn fur seals alive longer than 25 days. In the

Table 4

GENERAL FORMULA AND INGREDIENTS FOR ARTIFICIAL SEAL MILK, 1967

Component	Amount (%)
Protein	
Fish flour (fine grind for animal use, 73% protein)[a]	9.1
Casein (85% protein)[b]	4.5
Fat	
Whale oil (baleen, bleached triglyceride)[c]	36.0
Water	49.5
Supplement	
BO-SE (R)[d] selenium, and	0.00001
d-alpha tocopherol	0.0075
DL methionine[b]	0.4
Glycerin[e]	0.4
Antioxidant	
Ethoxyquin (Santoquin (R))[f]	0.01
Emulsifier	
Lecithin (soybean, oil not removed)[b]	0.1

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a. VioBin Corp., Monticello, Illinois.

b. Nutritional Biochemicals Corp., Cleveland, Ohio.

c. Del Monte Fishing Co., San Francisco, California, and Technology Laboratory, BCF, Seattle, Washington.

d. Haver Lockhart, Kansas City, Missouri.

e. Colgate-Palmolive Co., New York, New York.

f. Monsanto Chemical Co., St. Louis, Missouri.

first trials after the addition of fish flour to the diet, 13 of 16 newborn fur seals gained weight and, in spite of the stresses of early weaning, lived up to five months.

Fish flour was tried because it had been used successfully in milk-replacer diets for human infants (Levin, 1963) and baby pigs (Harmon, 1964), and seemed to be a logical source of protein for the young of a fish-eating animal. It is rich in B vitamins,[3] has an amino acid composition similar to that of fur seal milk, and may contain unknown growth factors required by seals. Fish flour has several advantages over fresh fish: Fish flour is easy to transport, store, and use for making formula; any measured amount contains all of the solid constituents of whole fish in natural proportions, and there is a high degree of uniformity throughout a batch and between batches; it does not contain thiaminase or viable intermediate stages of parasites, and, if handled properly, does not contain pathogenic microorganisms; it is not subject to rapid deteriorative changes which can either destroy nutrients or produce toxic elements; and finally, it is inexpensive and readily available.

Fats

Oil from fur seal blubber was the first fat to be tried, because the natural milk fats are undoubtedly mobilized from this source (Amoroso and Mathews, 1951). The main disadvantage of seal blubber oil was that it was unavailable commercially. Extraction from blubber by hand is slow and tedious. Menhaden oil (bleached and distilled triglyceride)[4] was tried because of its obvious relationship to the natural source of fat for pinnipeds. I also experimented with corn, safflower, and codliver oils.

Whale oil, tested at the same time as fish flour, gave better results than menhaden oil. It was available commercially and had already been used successfully by Hubbard in a formula for Steller sea lion pups (Poulter et al., 1965). The fatty acid composition of whale oil is similar to that of seal oil and other marine oils, i.e., predominantly long chain and polyunsaturated. Currently, I use whale oil that is bleached but not distilled. Distillation removes natural oil-soluble vitamins. Although bleaching is ordinarily used to remove color, the purpose here is to reduce the content of peroxides and other impurities. The bleached oil is stored in tins charged with nitrogen to prevent oxidation.

Emulsifier

If the fat is not emulsified it separates out in the stomach, is regurgitated and inhaled, and causes fatal foreign-body pneumonia.

Antioxidant

To minimize the oxidation of fats between mixing and digestion, ethoxyquin is added. I have not yet tried to measure the benefit of this practice.

Supplements

Vitamin E, selenium, and methionine were added to the formula because diets high in polyunsaturated fats require relatively high levels of vitamin E, and vitamin E is potentiated by selenium and methionine (Witting and Horwitt, 1964). Glycerin enables some animals to utilize free fatty acids in a carbohydrate-free diet (Renner, 1964). Because of the high vitamin and mineral content of fish flour and whale oil no other supplements were added. The purpose of the feeding trial in 1967 was to test the theoretical need to use vitamin E, selenium, methionine, and glycerin. By the end of the third week it was obvious that they were beneficial. Five of six pups not on supplement died, and four of six pups on supplement survived.

Antibiotics

In the 1965 feeding trials with 24 newborn fur seals there was no observable difference in the weight gain or longevity between the 12 pups that received daily, low-level, broad-spectrum antibiotics and the 12 that did not. Therefore, antibiotics are not added as a prophylactic measure. Such a practice leads to alteration of the natural flora of the digestive tract and may bring about the evolution of resistant pathogens.

Preparation of Formula and Feeding

Ingredients can be stored at room temperature but formula should be fed within an hour after it is prepared. The proetins and water are mixed in a blender for 10 to 15 seconds. The mixture of fat, emulsifier, and antioxidant are blended separately for 5 to 10 seconds. Then the two mixtures are blended together for 10 to 15 seconds. Supplement is calculated on an individual per feeding basis and added separately.

Each pup is started on 60 ml of formula twice a day. This amount is increased 10 ml/feeding until 120 ml twice a day is reached. On the fourteenth day the amount per feeding is increased to 130 ml and by the twenty-fifth day to a maximum of 150 ml twice daily. By the fortieth day the schedule can be gradually converted to 300 ml once a day. During the first week pups lose about 0.5 kg of body weight as their system adjusts to the artificial diet. At the end of the second week their weight should be the same as at the end of the first week. They should then gain about 0.5 kg/week for several weeks.

Although fur seal pups can eventually be taught to nurse an artificial nipple (real seal milk and a natural skin through which to offer the nipple are good aids), it is more practical when working with more than two or three animals to feed by stomach tube. The proper material and technique for this method have been described by Wilson (1966).

Hazards to Health

The greatest hazard to the health of captive newborn seals is overfeeding, which results in indigestion, vomiting, and subsequent electrolyte imbalance, dehydration, coma, and death. At this point the question of electrolyte intake and excretion by artificially fed pups should be mentioned. The best results of feeding trials of newborn fur seals were obtained with formula to which no electrolyte was added other than that which naturally occurs in the ingredients. Furthermore, they began to gain weight 15 days before they had access to seawater. Nevertheless, in three separate trials pups have seemed more lively after they were given access to seawater, and some pups did appear to be drinking it. If excretion of electrolyte is constant in seals and to some degree similar to this mechanism in albatrosses, there should be some provision for replenishing the excreted electrolyte. One mechanism pinnipeds have for salt excretion is through their tears, which flow copiously and streak the otherwise dry face and neck of the animals while they are on land. Terrestrial mammals that need to conserve salt swallow their tears, which reach the throat through nasolachrymal ducts (these ducts are absent in pinnipeds).

Next to overfeeding the most important hazard to health is soiling of the fur, which leads to chilling and death. Soiling can be prevented by the use of wood slat flooring and a tank for bathing (Fig. 1).

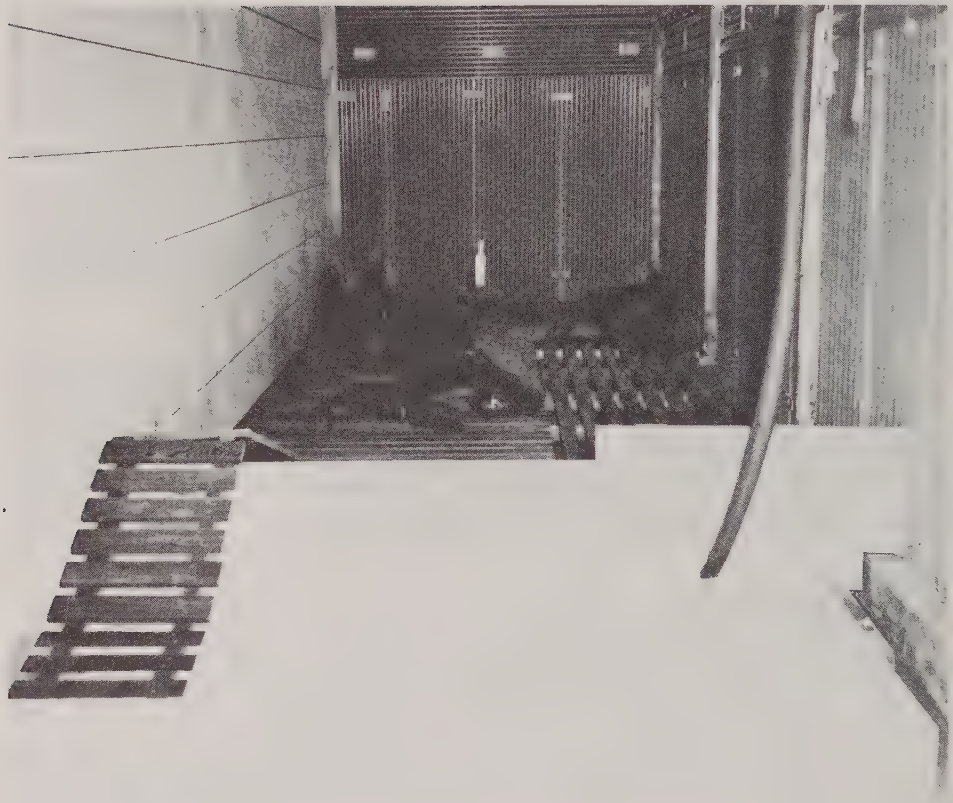

Fig. 1 PUP ENCLOSURE WITH WOOD SLAT FLOORING AND BATHING TANK.

Inhalation of formula during feeding, or after regurgitation, is an important hazard because it causes death from foreign-body pneumonia.

Newborn fur seals are usually exposed to hookworm larvae in their first milk. If such pups are not successfully wormed, they may die of anemia.

Steller Sea Lion *(Eumetopias jubatus)*

The development of a formula and husbandry practice to successfully rear, for the first time, orphaned Steller sea lion pups to over one year of age has been described by Poulter et al. (1965). The first successful formula, developed in 1964, contained the following ingredients per liter:

Casein	75 g
Whipping cream	200 ml
Whale oil	300 ml
Glucose (50%)	1 ml
NaCl	1 tsp
Water	q.s. 1 liter

After two months on this diet blended mackerel was added gradually over a two-week period until it reached a level of 180 g/liter.

Several changes in this formula have been made over the last three years; the current formula is as follows:

Blended mackerel (headless)	220 g
Fish flour	80 g
Whale oil (light baleen)	350 ml
Water	350 ml
Vitamin-mineral (Gerex-Walins)	6 capsules
U.S.P. salt mixture XIV	1 g
	1,000 g

California Sea Lion *(Zalophus californianus)*

Howard Baldwin, Director of Sensory Systems Laboratory, Tucson, Arizona, kept three young[5] California sea lions for four months during which time they gained about 5 kg each. They were fed formula and fresh fish, starting with 120 to 180 g formula and one small fish (smelt) twice a day. The amount of fish was gradually increased to 500 to 700 g ground fish fed with a caulking gun twice a day. By the third month they were each receiving about 2 kg of ground fish per day. With some difficulty they were taught to eat whole fish. The formula consisted of 300 g cod liver oil and 150 g calcium caseinate (Casec (R))[6] mixed in 500 ml of water (Baldwin, 1968, personal communication).

Harbor Seal *(Phoca vitulina)*

No large-scale feeding trials have been conducted for the purpose of developing a formula that will sustain harbor seal pups without the early introduction of raw fish. Since the nursing period is so short (about three weeks), it must serve the primary purpose of allowing the pup to build up a reserve of blubber that will tide him over until he has learned to catch and swallow small fish and other marine organisms. If the proper forms of such marine life are made available to the pup (as in the captive situation), the need for a nursing formula is greatly diminished. If small forms of marine life are not available, good results may be obtained by using blended fresh fish mixed with warm water and multivitamins (Reineck, 1962). Many harbor seal pups have undoubtedly survived in spite of, rather than because of, formula containing bovine milk and other unnatural substances because their captors sensed the need to introduce fresh fish early.

Northern Elephant Seal *(Mirounga angustirostris)*

To my knowledge, no newborn elephant seals have ever been reared in captivity, but Peter Batten of the Kelly Park Zoo, San Jose, California, has successfully fed very young calves a formula similar to that used for northern fur seals. Hubbard has used his Steller sea lion formula for this purpose.

Walrus *(Odobenus rosmarus)*

Brown (1962) and Brown and Asper (1966) give a thorough coverage of the diet and growth of captive walrus calves.

FOOTNOTES

1. Adapted from data of T. Scheffer and Sperry (1931) by V. Scheffer and Slipp (1944).

2. The pup was reared by me on St. Paul Island for the first 35 days, then by R. C. Hubbard at Stanford Research Institute, Coyote Hills, California.

3. Analysis of fish flour, the VioBin Corporation, Monticello, Illinois.

4. Processed by the Bureau of Commercial Fisheries Technology Laboratory, Seattle, Washington. In the bleaching process, the oil is mixed with activated clay and charcoal and is agitated under vacuum at 60° to 70°C.

5. The sea lions were not newborn; they weighed between 11.5 and 17 kg.

6. Meade Johnson.

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Pasteurella multocida Isolated from a California Sea Lion *(Zalophus californianus)*

Mark C. Keyes, D.V.M.; Frank W. Crews, Ph.D.; A. John Ross, M.S.

On Oct. 7, 1963, a 2-year-old male California sea lion (*Zalophus californianus*), belonging to the Seattle Marine Aquarium, died suddenly after having occasional fainting spells for about 3 months.

Necropsy Findings

The sea lion's weight (45 kg.) was normal for its size; it had a heavy layer of blubber. The pleural cavity was completely filled with turbid, yellowish fluid bearing large flecks of puslike material, a sample of which was taken for culture. There were numerous large adhesions between the pericardium, which was thickened, and the acutely inflamed pleura. The brachial lymph nodes were dark and mottled. The epiglottis was edematous, and the larynx contained heavy mucus. The heart was enlarged and flabby. There were lenticular cataracts in both eyes. The abdominal viscera appeared normal except for the stomach which was filled with an almost clear yellow fluid.

Microbiologic Findings

The primary isolant was obtained in pure culture at the Western Fish Disease Laboratory by incubation at 37 C. on 5% blood agar and trypticase soy broth plus 2% sodium chloride. On solid medium, cells grew as small cocci, coccobacilli, and small bacilli (Fig. 1). Filamentous forms were most common in broth cultures (Fig. 2). Cells changed from one form to the other on change from one type of medium to the other, but filamentous forms were not found in broth to which NaCl had not been added. Because of the pleomorphic nature of the organism and the findings at necropsy, a mycoplasma was suspected.

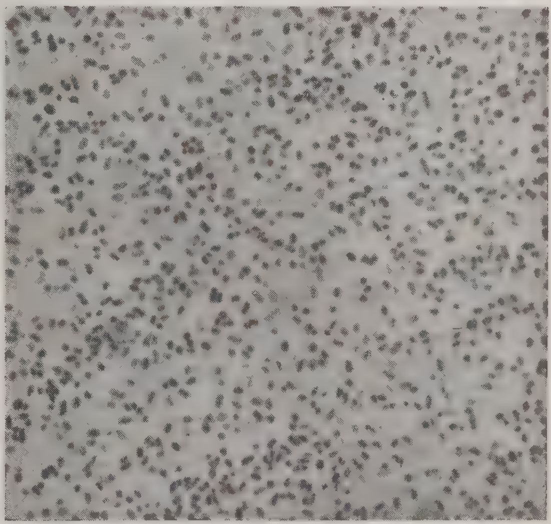
Fig. 1—Sea lion bacteria grown on 5% blood agar with 2% NaCl added. Gram stain; x 2,400.

Subcultures of the organism were sent to the Washington State Department of Agriculture Laboratory for further study. Here the organism grew abundantly on

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Dr. Keyes is with the Department of the Interior, U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries, Marine Mammal Biological Laboratory, Seattle, Wash.; Dr. Crews is supervisor of the State of Washington Department of Agriculture Laboratory, Olympia, Wash.; and Mr. Ross is bacteriologist for the Department of the Interior, U.S. Fish and Wildlife Service, Bureau of Sport Fisheries and Wildlife, Western Fish Disease Laboratory, Seattle, Wash.

The authors thank Dr. L. A. Page and Mr. Kenneth Heddleston of the National Animal Disease Laboratory; Dr. Robert E. Weaver and his staff at the National Communicable Disease Center; Dr. Louis N. Locke of the Patuxent Wildlife Research Center; the National Institute of Health Clinical Bacteriology Laboratory for positive identification; and W. T. Yasutake, Western Fish Disease Laboratory for photomicrography.

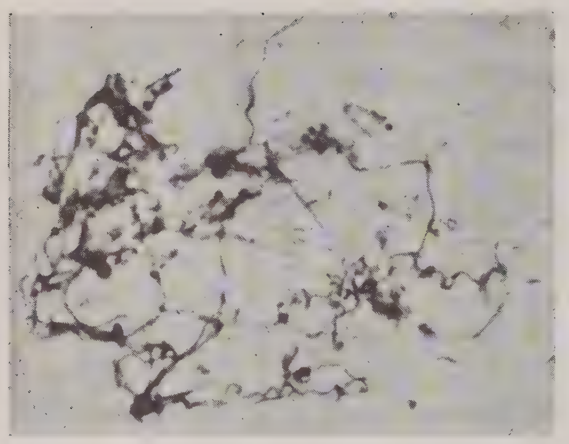

Fig. 2—Sea lion bacteria grown in trypticase soy broth with 2% NaCl added. Gram stain; x 2,400.

TABLE 1—Essential Biochemical Properties of a Sea Lion Bacterium Incubated 96 Hours at 37 C.

Test	Reaction
SSS Fe agar	Acid, H_2S not produced, slow fermentation
Indol*	Slow positive
Methyl red	Negative
Voges-Proskaur	Negative
Sodium citrate	Negative
Urea hydrolysis buffered	Negative
Urea hydrolysis unbuffered*	Slow positive
Nitrate reduction	Strongly positive
Gelatinase	Negative
VRB Lactose agar	No growth
Litmus milk	No change
Methylene Blue Milk 1:5,000	No change
Catalase production	Positive (strongly)
Lactose	Slight acid, no gas
Sucrose	Acid, no gas
Dextrose	Acid, no gas
Maltose	Slow acid, no gas
Raffinose	No acid or gas
Rhamnose	No acid or gas
Galactose	Acid, no gas
Sorbitol	Acid, no gas
Glycerol	Acid, no gas
Fructose	Acid, no gas

* Eight-day incubation.

bovine blood agar, liver infusion agar, and brain-heart infusion agar within 48 hours at 37 C. It was nonhemolytic on bovine blood agar. On these mediums the cells were coccoid and about 0.1 to 0.5 μ in length. Some filaments were also found. Colonies were small (<0.5 mm. in diameter) and transparent, with a raised center gradually developing. The surfaces became rough with age, and in some instances small "daughter" colonies surrounded areas of initial growth. After prolonged incubation in fluid medium, cells were filamentous, but small cells also occurred, varying in length from approximately 0.1 to 1.0 μ. All cells were gram-negative, nonsporulated, and nonmotile. Morphologically, the organisms resembled members of the families Mycoplasmataceaea and Brucellaceaea. Biochemical properties of the organism (Table 1) were also suggestive of Mycoplasmataceaea and Brucellaceaea.

Lyophilized samples were sent to the National Animal Disease Laboratory, Ames, Iowa, the National Communicable Disease Center, Atlanta, Ga., and the National Institute of Health, Bethesda, Md., each of which identified the organism as *Pasteurella multocida*.

Discussion

On the basis of the necropsy and bacteriologic findings, the identity of the organism was narrowed to the families Mycoplasmataceaea and Brucellaceaea. It differed from *Mycoplasma mycoides* in certain biochemical properties, *i.e.*, positive indole, urea hydrolysis, nitrate reduction, and catalase tests.[1] Mycoplasma of bovine pleuropneumonia cases have been negative in these tests, with the exception of slow nitrate reduction and variable to negative catalase production. This culture slowly developed urease, with a positive test at 8 days or more of incubation at 37 C. This property usually is not attributed to pasteurella organisms. Urea hydrolysis was not reported on by all of the laboratories.

In fluid-medium cultures of mycoplasma of bovine origin, there is usually cell capsulation and gradual massive clustering of cells. This organism from the sea lion did not have these growth characteristics.

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[1] Breed, Robert S., Murray, E.G.D., and Smith, Nathan R.; Bergey's Manual of Determinative Bacteriology. 7th ed. Wliliams & Wilkins Company, Baltimore, Md., 1957.

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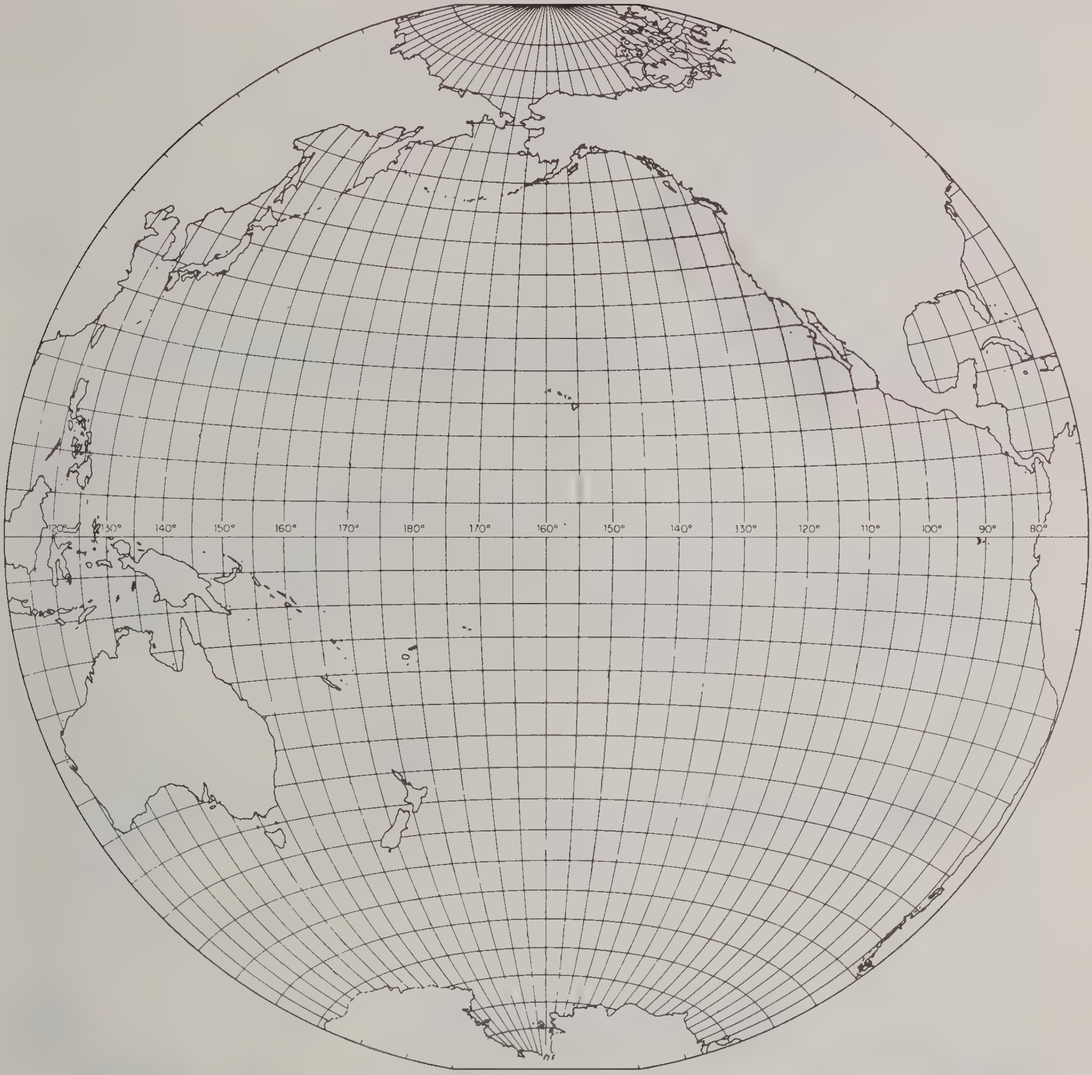
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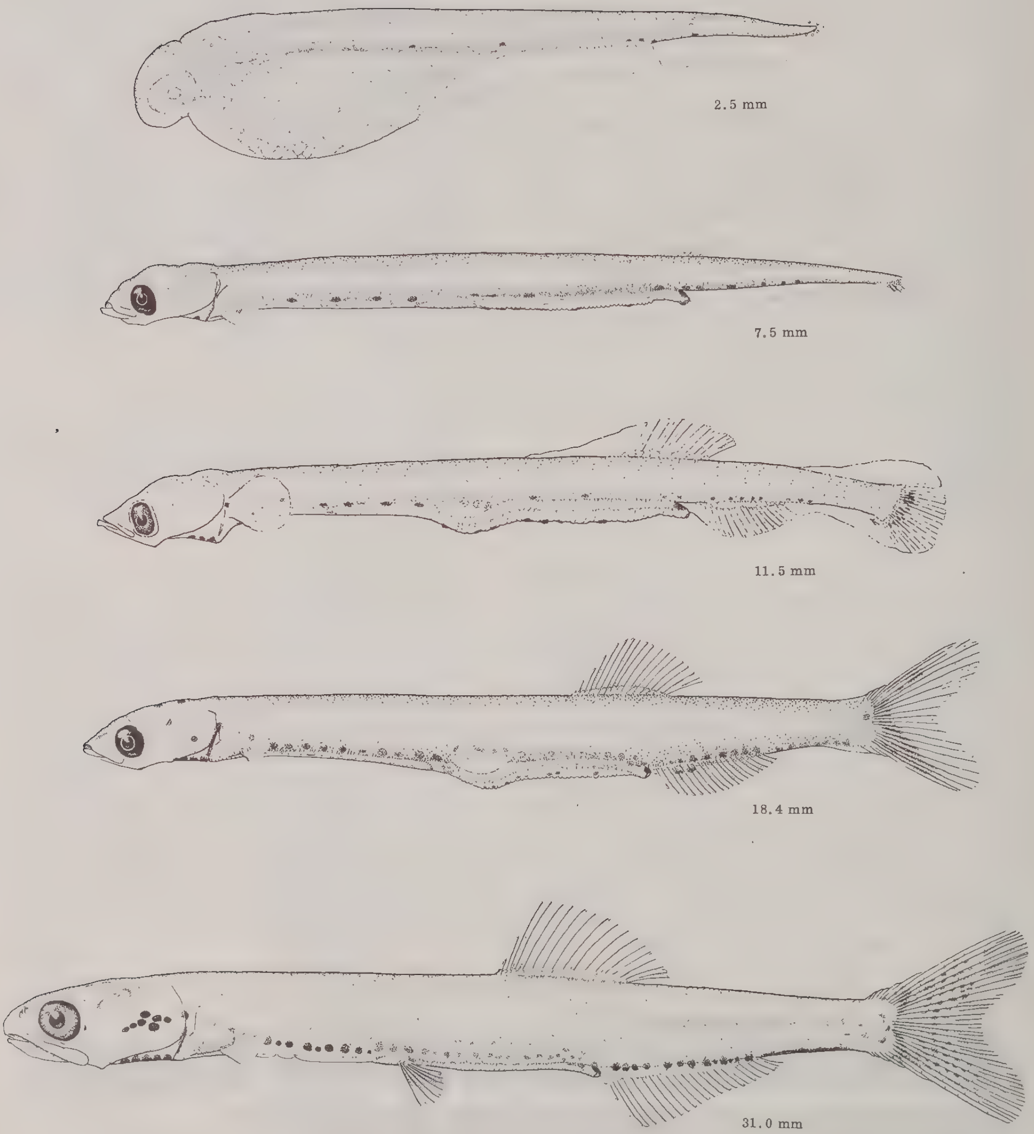
CALIFORNIA COOPERATIVE OCEANIC FISHERIES INVESTIGATIONS

ATLAS No. 9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NORTHERN ANCHOVY

Engraulis mordax

CALIFORNIA COOPERATIVE OCEANIC FISHERIES INVESTIGATIONS

Atlas No. 9

STATE OF CALIFORNIA
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March, 1968

THE CALCOFI ATLAS SERIES

This is the ninth in a series of atlases containing data on the hydrography and plankton from the region of the California Current. The field work was carried out by the California Cooperative Oceanic Fisheries Investigations,[1] a program sponsored by the state of California under the direction of the State's Marine Research Committee. The cooperating agencies in the program are:

California Academy of Sciences
California Department of Fish and Game
Stanford University, Hopkins Marine Station
U. S. Fish and Wildlife Service, Bureau of Commercial Fisheries
University of California, Scripps Institution of Oceanography

CalCOFI atlases[2] are issued as individual units as they become available. They provide processed physical, chemical and biological measurements of the California Current region. Each number may contain one or more contributions. A general description of the CalCOFI Program with its objectives appears in the preface of Atlas No. 2.

This atlas was prepared by the Data Collection and Processing Group of the Marine Life Research Program, Scripps Institution of Oceanography.

CalCOFI Atlas Editorial Staff:

Abraham Fleminger and Hans T. Klein, Editors
John G. Wyllie, Cartographer

Atlases in this series, through March 1968, are:

CalCOFI Atlas No. 1
Anonymous. CalCOFI atlas of 10-meter temperatures and salinities 1949 through 1959.

CalCOFI Atlas No. 2
Fleminger, A. Distributional atlas of calanoid copepods in the California Current region, Part I.

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CalCOFI Atlas No. 9
Kramer, D., and E. H. Ahlstrom. Distributional atlas of fish larvae in the California Current region: Northern Anchovy, *Engraulis mordax* Girard, 1951 through 1965.

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[1] Usually abbreviated CalCOFI, sometimes CALCOFI or CCOFI.

[2] For citation this issue in the series should be referred to as CalCOFI Atlas No. 9.

DISTRIBUTIONAL ATLAS OF FISH LARVAE IN THE CALIFORNIA CURRENT REGION: NORTHERN ANCHOVY, ENGRAULIS MORDAX GIRARD, 1951 THROUGH 1965

David Kramer[1] and Elbert H. Ahlstrom[1]

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Charts 1-269

Introduction to the Charts

This atlas depicts the abundance and distribution of the larvae of the northern anchovy, Engraulis mordax Girard, in the region of the California Current off California and Baja California. The charts include the data collected on all cruises (exclusive of special surveys and special stations) conducted by the California Cooperative Oceanic Fisheries Investigations during the years 1951 through 1965 (Ahlstrom, 1953, 1954; Ahlstrom and Kramer, 1955, 1956, 1957; Ahlstrom, 1958, MSS[2]). Surveys were conducted monthly during the decade 1951 through 1960 and quarterly during 1961 through 1965. Details of sampling methods were described by Ahlstrom (1948, 1953) and Fleminger (1964). Briefly, each sample was collected with the standard CalCOFI net constructed of silk mesh (bolting cloth), mouth diameter one meter and mesh size approximately 0.55 mm. Occasionally, a nylon net of the same mouth opening and mesh size was used. A flowmeter in the mouth of the net permitted calculation of the amount of water strained. Each tow was made by sinking the net at 50 meters per minute to a depth of about 140 meters (200 meters of wire out, depth permitting) and by retrieving it at 20 meters per minute while maintaining a wire angle of 45 degrees. The ship's speed during the tow was about 2 knots.

In the laboratory, samples were sorted for all fish eggs and larvae. In the case of a very large-sized sample examination was made of an aliquot obtained from the Folsom Plankton Sample Splitter (McEwen, Johnson and Folsom, 1954).

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[1] Fishery-Oceanography Center, U. S. Bureau of Commercial Fisheries, La Jolla, California.

[2] Ahlstrom, MSS are preliminary data reports (1) for 1958 and 1959, and (2) for 1960 through 1964, prepared at the Fishery-Oceanography Center for limited distribution. The data for 1965 have not been released before.

The standardized values for fish eggs and larvae are not directly comparable with the standardized values used by authors of previous CalCOFI atlases, where the values were adjusted to volume of water strained. For most stations, the standardized values for anchovies are approximately 1.4 times as large.

Estimates of abundance of larvae and eggs were made comparable between samples by standardizing the values to a unit of ten square meters of sea surface. The standardization factor was derived for each station according to the volume of water strained and the average depth of each haul as follows:

$$S = \frac{10\,D}{V} \text{ or } \frac{10\,D}{Rap}, \tag{1}$$

where

S = standardized haul factor,

D = average depth of a haul in meters,

V = number of cubic meters of water strained during a haul,

R = number of revolutions registered by the current meter during a haul,

a = cross-sectional area of the net mouth in square meters, and

p = length of the column of water in meters needed to effect one revolution of the current meter at the average speed at which the haul was taken.

Note that

$$V = Rap. \tag{2}$$

The contour intervals of the present charts also differ from those used in previous CalCOFI atlases. Since anchovy larvae are seldom collected in numbers greater than 10,000, and since five contour intervals were desired, each interval was reduced to one-fifth of that used in CalCOFI Atlases 2, 3, 5, 6, 7 and 8.

The strata occupied by anchovy larvae are completely sampled by the standard haul from the surface to 140 meters of depth (Ahlstrom, 1959b). It is known, however, that larvae of various sizes are able to escape the net. Small ones may pass through the 0.55-mm mesh and large ones may swim away from the path of the net, especially during daylight. Therefore, two charts are presented for each cruise, one for the size group most adequately sampled (6.26-12.25 mm), and one for the total numbers caught.

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CalCOFI Basic Station Plan 1

Distribution of Northern Anchovy larvae 2-269. See table below for individual cruises

Months	01	02	03	04	05	06
Years						
1951	2, 3	4, 5	6, 7	8, 9	10, 11	12, 13
52	26, 27	28, 29	30, 31**	32, 33	34, 35	36, 37
53	48, 49	50, 51	52, 53**	54, 55	56, 57	58, 59
54	72, 73	74, 75	76, 77	78, 79	80, 81	82, 83
55	92, 93	94, 95	96, 97	98, 99	100, 101	102, 103
56	114, 115	116, 117	118, 119	120, 121	122, 123	124, 125
57	138, 139	140, 141	142, 143	144, 145	146, 147	148, 149
58	162, 163	164, 165	166, 167	168, 169	170, 171	172, 173
59	186, 187	188, 189	190, 191	192, 193	194, 195	196, 197
60	210, 211	212, 213	214, 215	216, 217	218, 219	220, 221
61	230, 231			232, 233		
62	238, 239			240, 241		
63	246, 247			248, 249		
64	254, 255			256, 257		
1965	262, 263			264, 265		

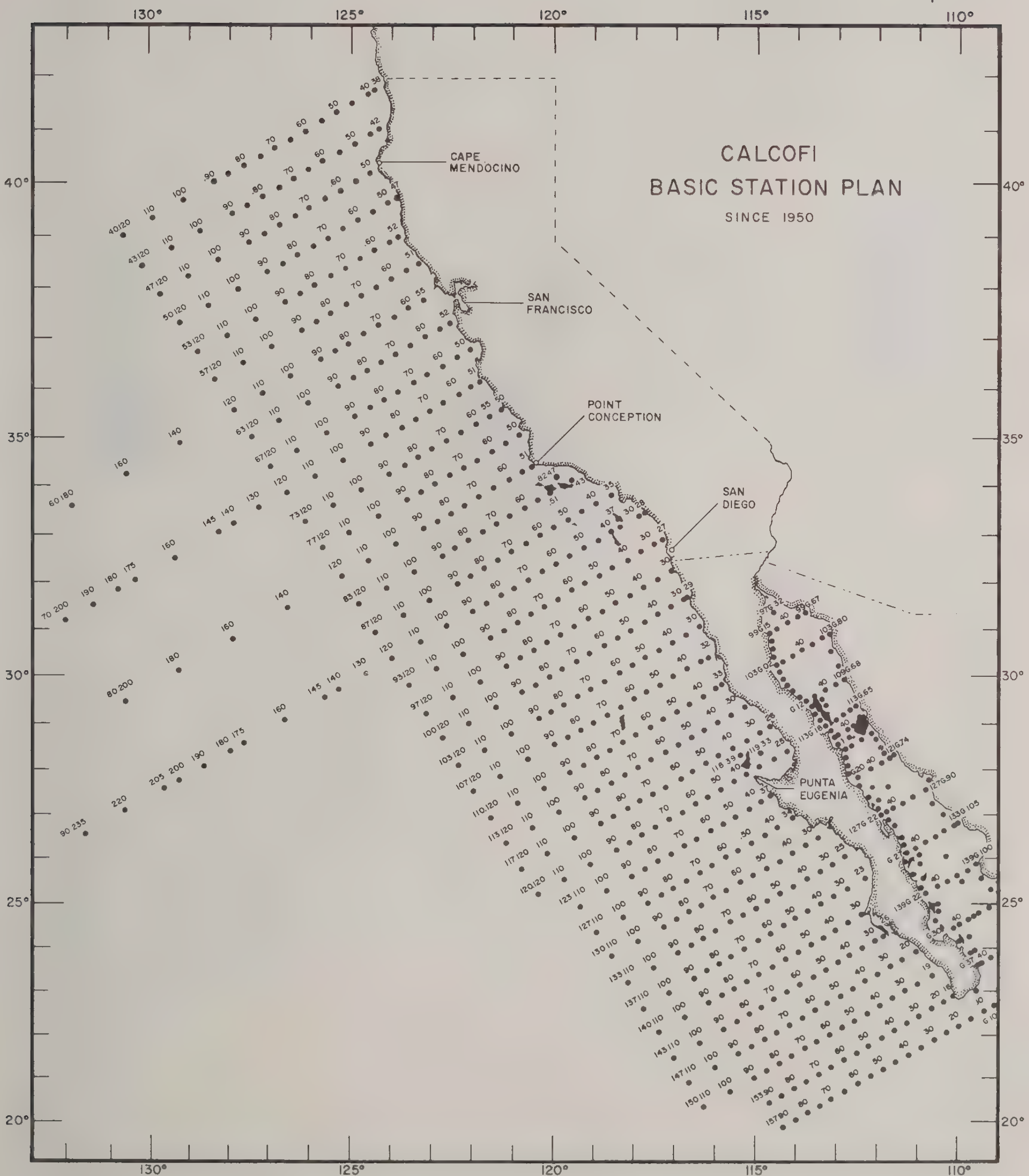
* The first two figures in the CalCOFI cruise-numbering system represent the year of the cruise; the last two figures, the month.

The table below is a cross reference to an earlier system of assigning cruise numbers. The earlier numbers are in parentheses.

5101 (21)
5102 (22)
5103 (23)
5104 (24)
5105 (25)
5106 (26)
5107 (27)
5108 (28)
5109 (29)
5110 (30)
5111 (31)
5112 (32)
5201 (33)
5202 (34)
5203 (35)
5203 (35)
5204 (36)
5205 (37)
5206 (38)
5207 (39)
5208 (40)
5209 (41)
5210 (42)
5211 (43)

07	08	09	10	11	12	Years
14, 15	16, 17	18, 19	20, 21	22, 23	24, 25	1951
38, 39	40, 41	42, 43	44, 45	46, 47		52
60, 61	62, 63	64, 65	66, 67	68, 69	70, 71	53
84, 85	86, 87		88, 89		90, 91	54
104, 105		106, 107	108, 109	110, 111	112, 113	55
126, 127	128, 129	130, 131	132, 133	134, 135	136, 137	56
150, 151	152, 153	154, 155	156, 157	158, 159	160, 161	57
174, 175	176, 177	178, 179	180, 181	182, 183	184, 185	58
198, 199	200, 201	202, 203	204, 205	206, 207	208, 209	59
222, 223	224, 225	226, 227	228, 229			60
234, 235			236, 237			61
242, 243			244, 245			62
250, 251			252, 253			63
258, 259			260, 261			64
266, 267		268, 269				1965

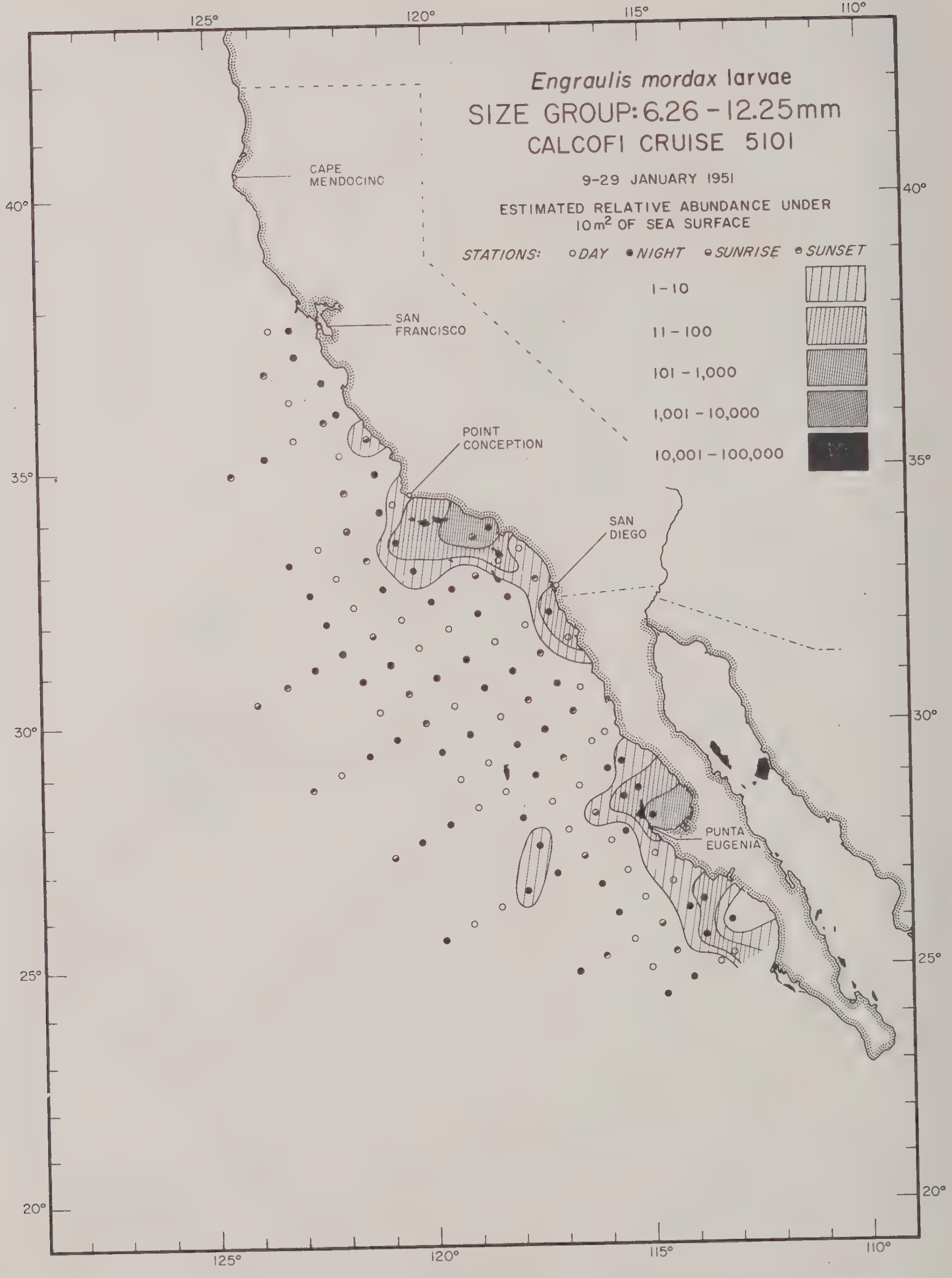
** In March 1952 and March 1953, surveys were conducted twice a month. The results of the repetitive cruises are shown separately on the same page.


130°
125°
120°
115°
110°
40°
35°
30°
25°
20°
CALCOFI
BASIC STATION PLAN
SINCE 1950
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

CALCOFI

BASIC STATION PLAN

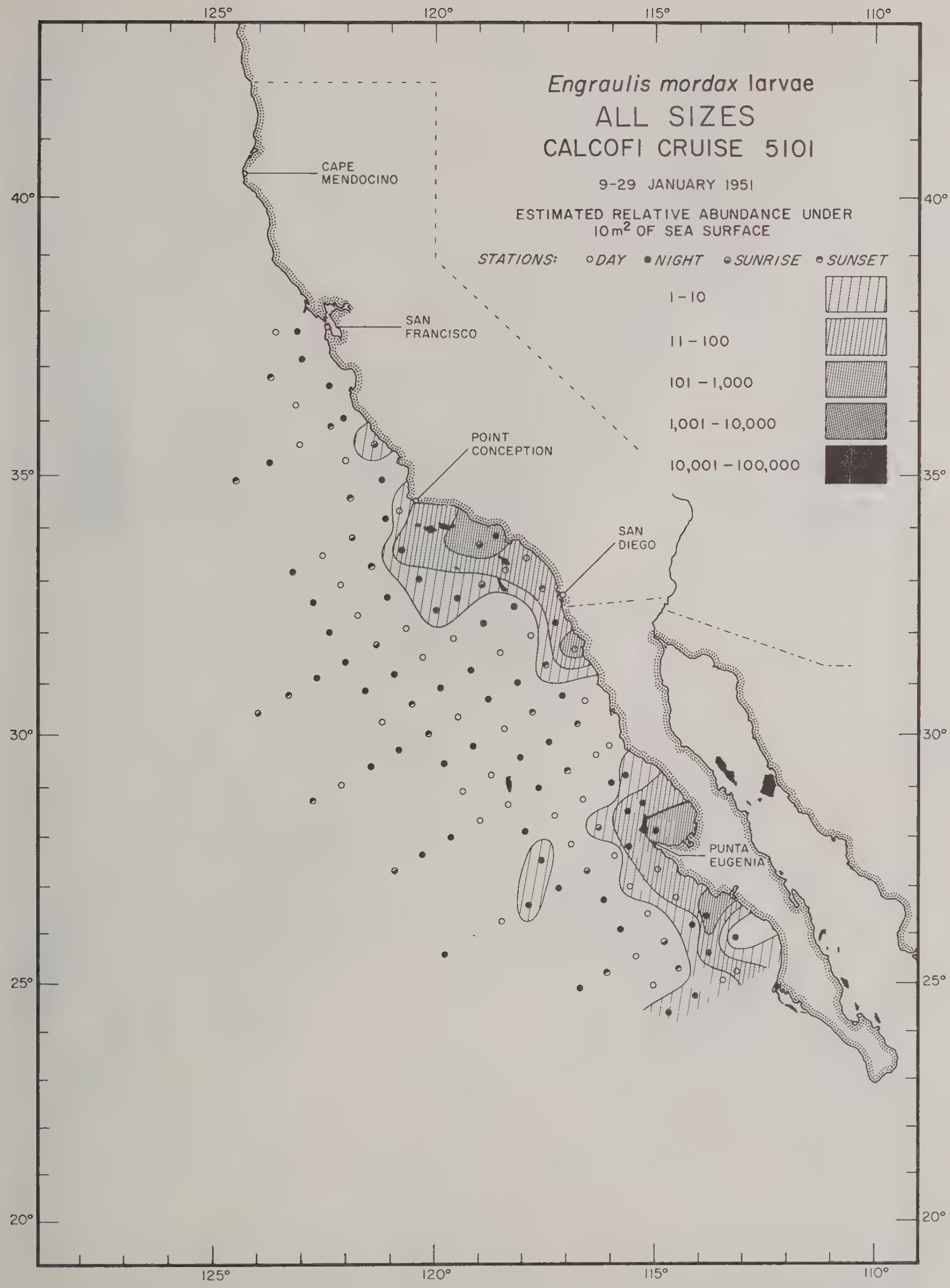
SINCE 1950


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5101
9-29 JANUARY 1951
ESTIMATED RELATIVE ABUNDANCE UNDER
$10\,m^2$ OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

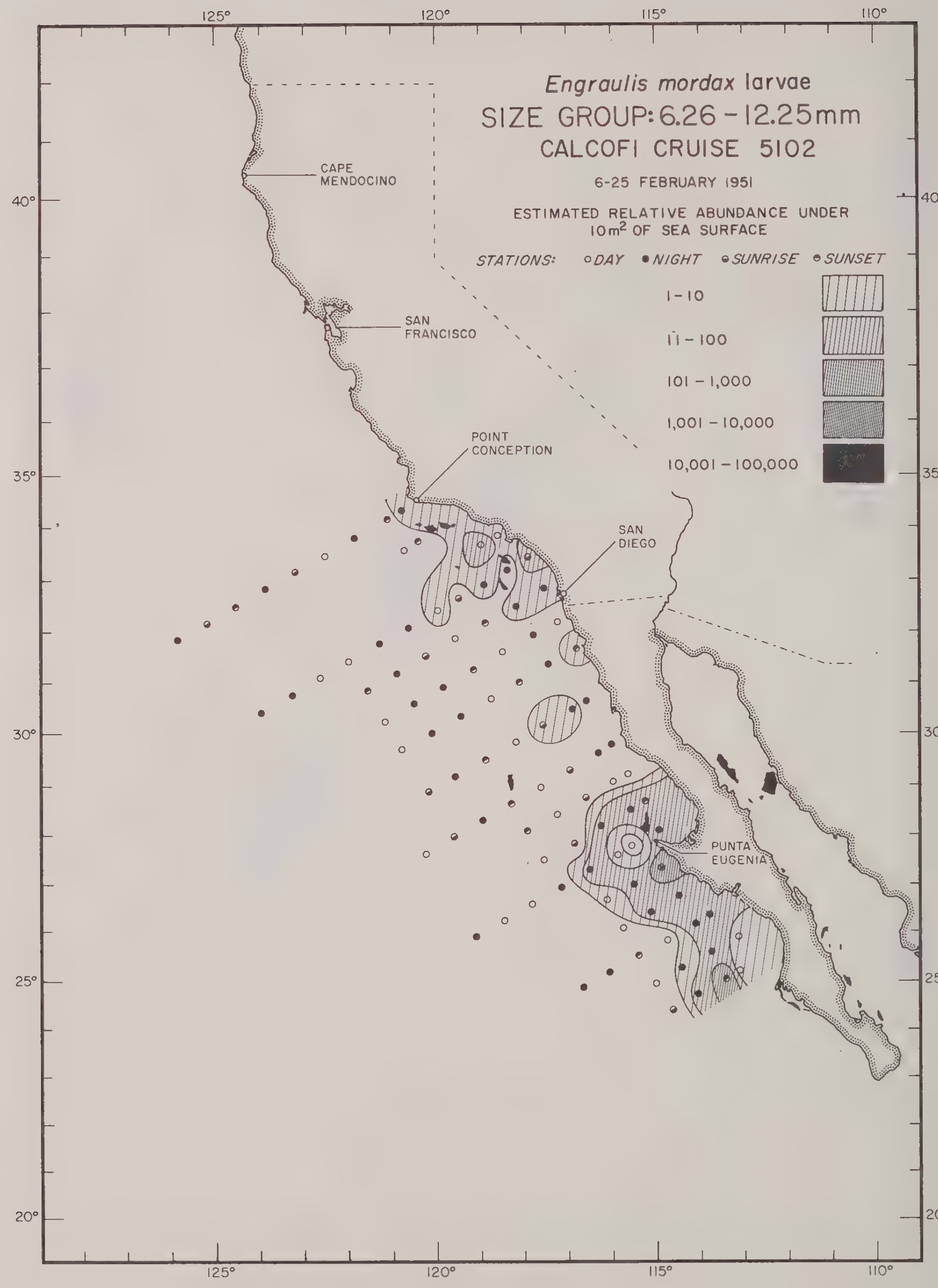
5101


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5101
9-29 JANUARY 1951
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

All Sizes

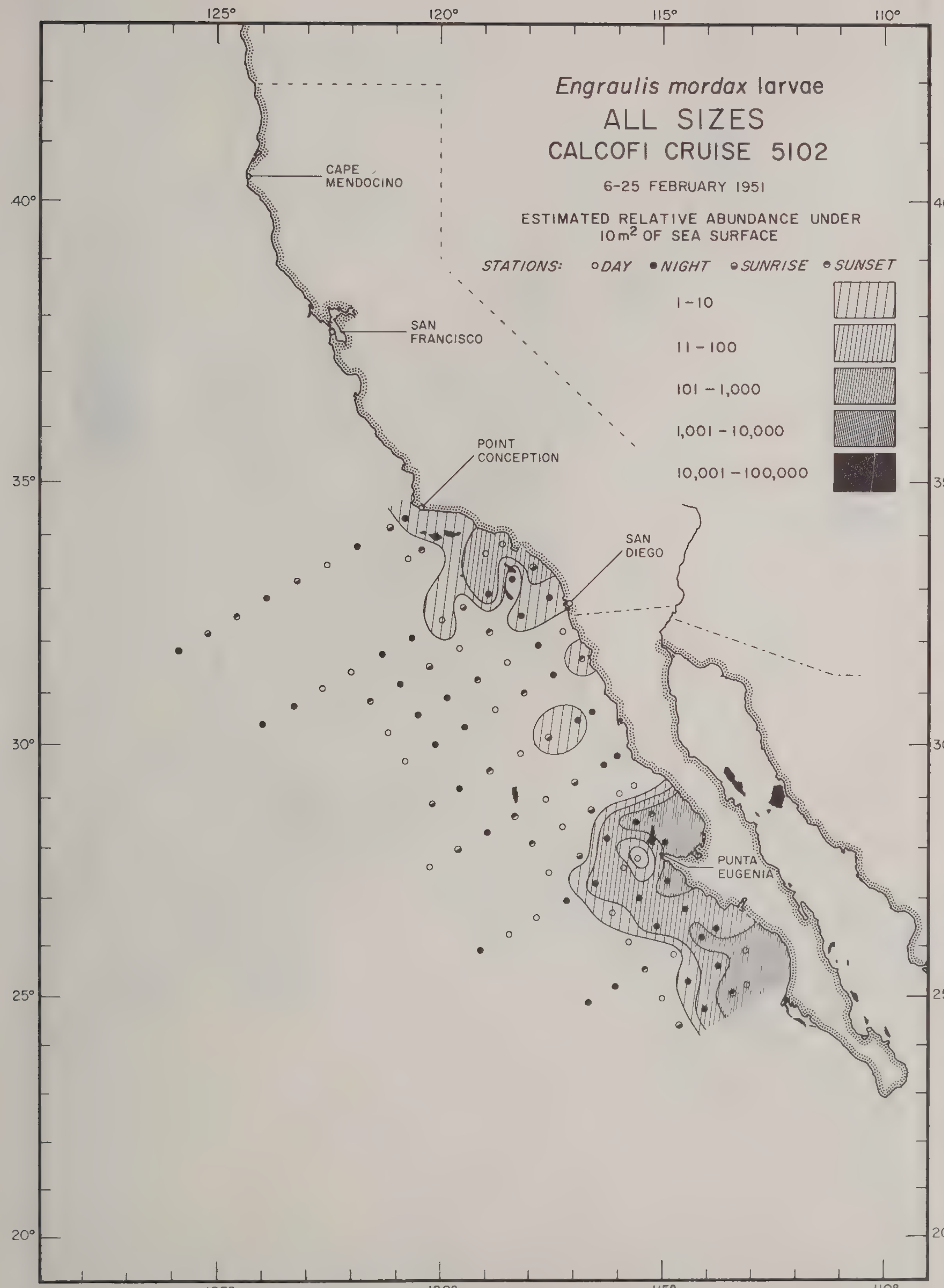
5101


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5102
6-25 FEBRUARY 1951
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

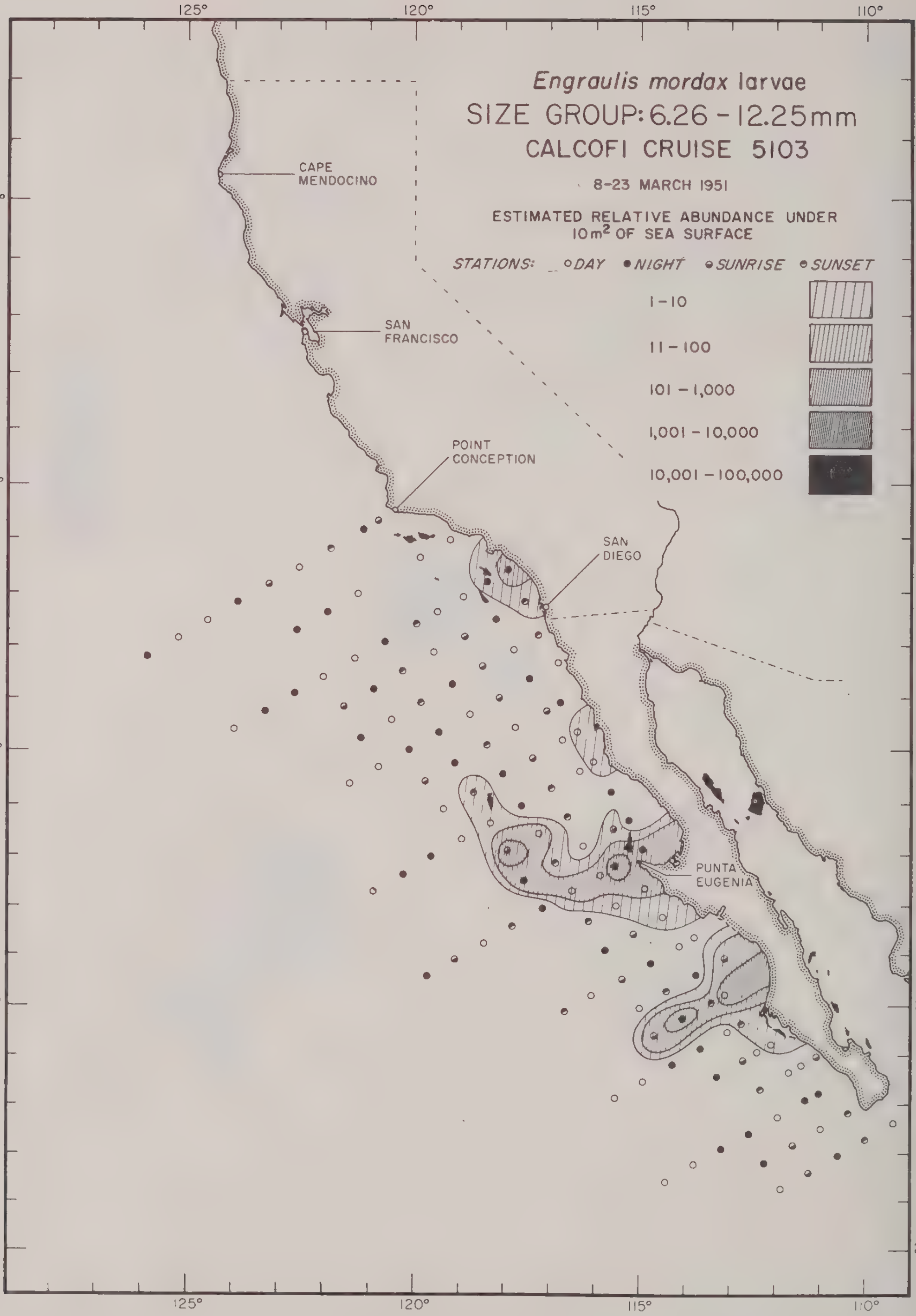
5102


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5102
6-25 FEBRUARY 1951
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ *DAY* ● *NIGHT* *SUNRISE* *SUNSET*
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

All Sizes

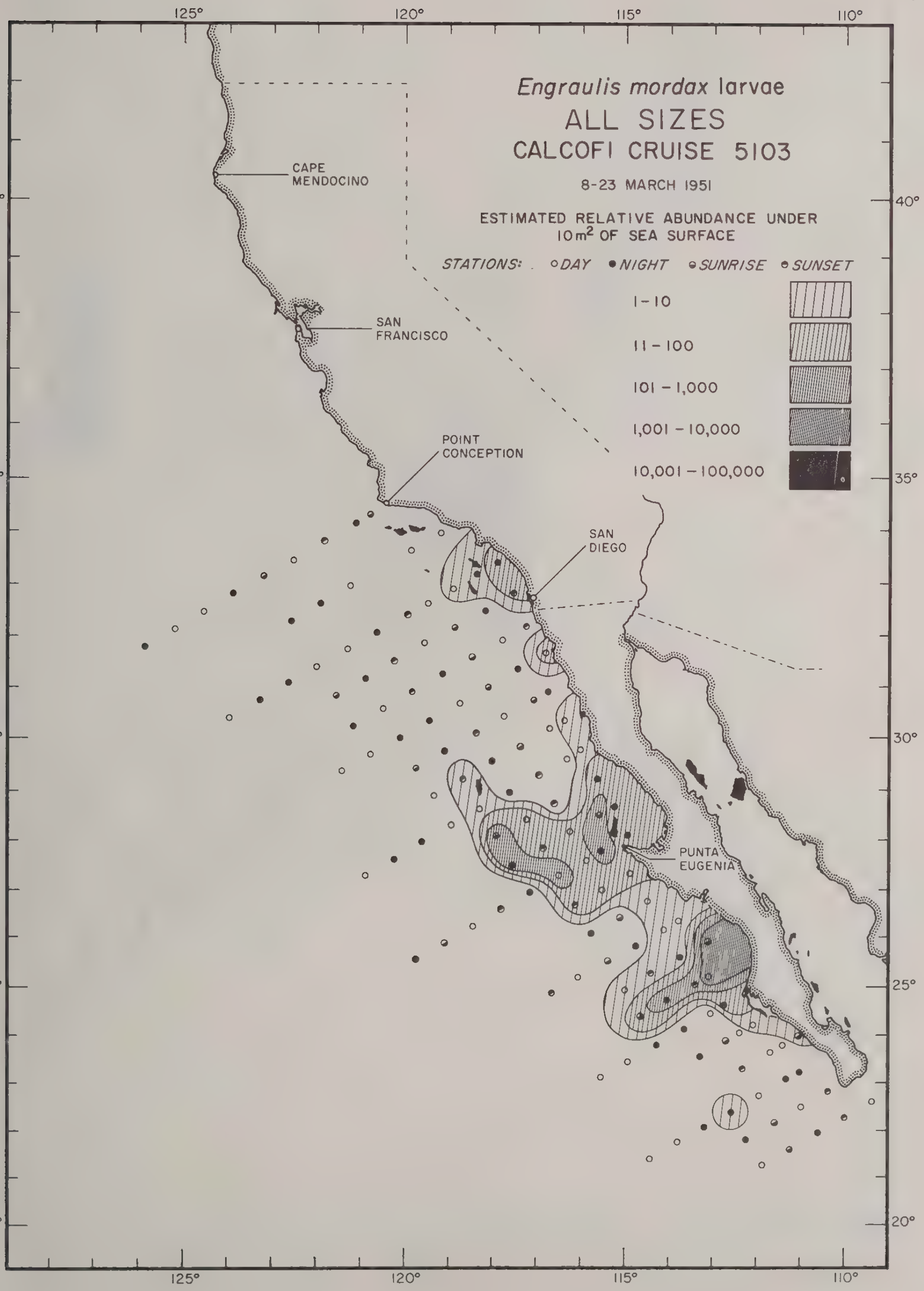
5102


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5103
8-23 MARCH 1951
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

Size Group: 6.26-12.25mm

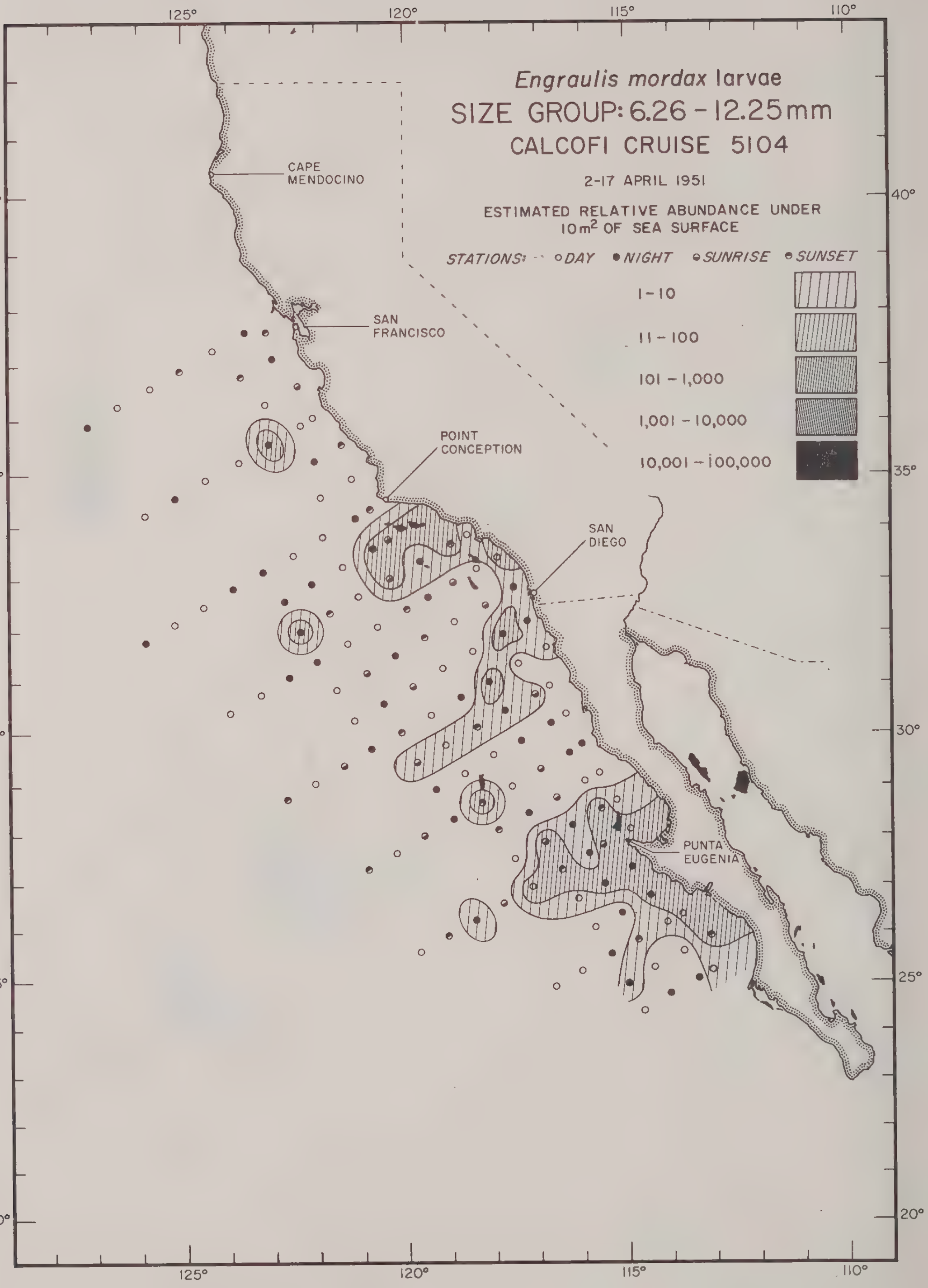
5103


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5103
8-23 MARCH 1951
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

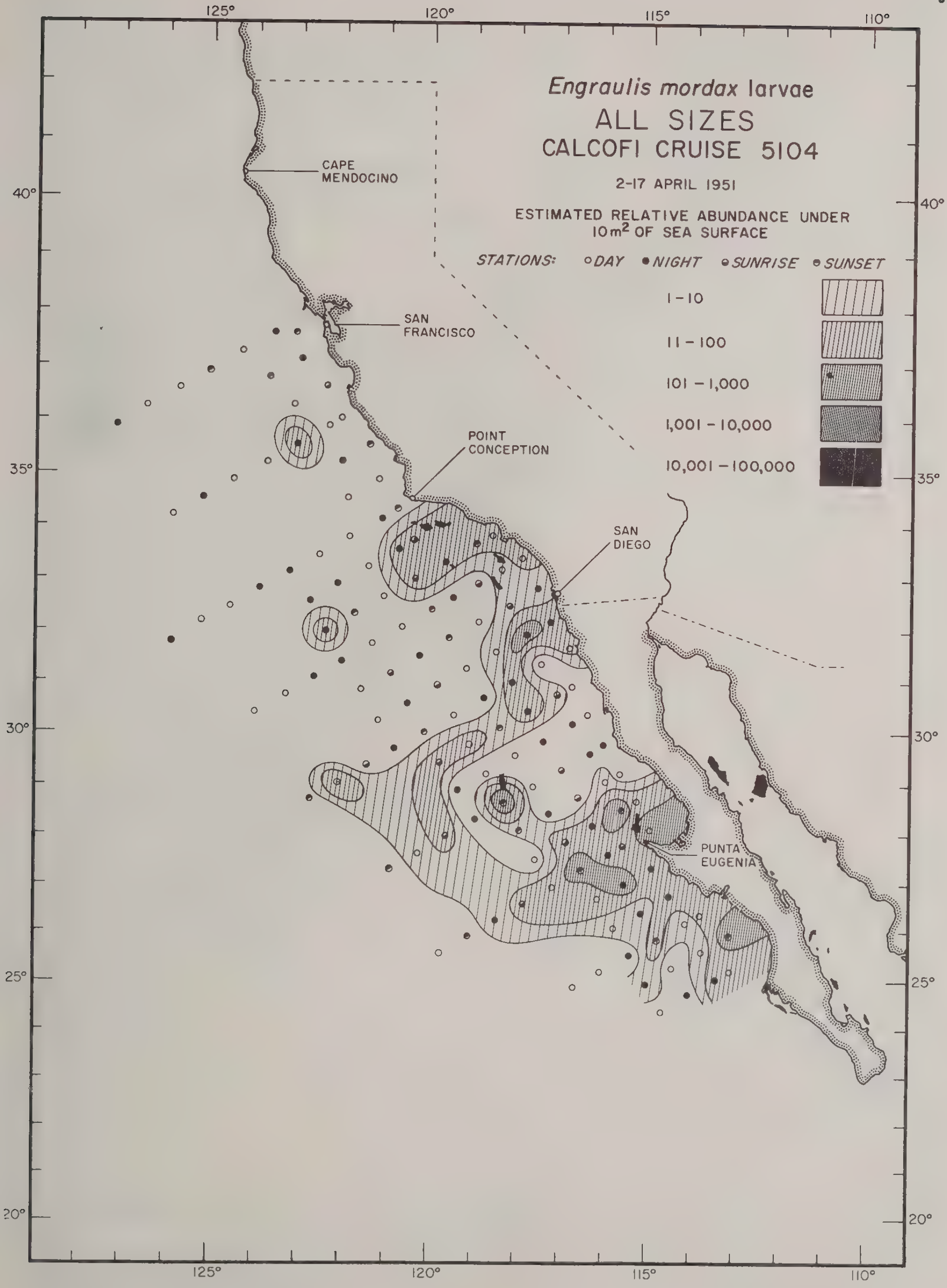
5103


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5104
2-17 APRIL 1951
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

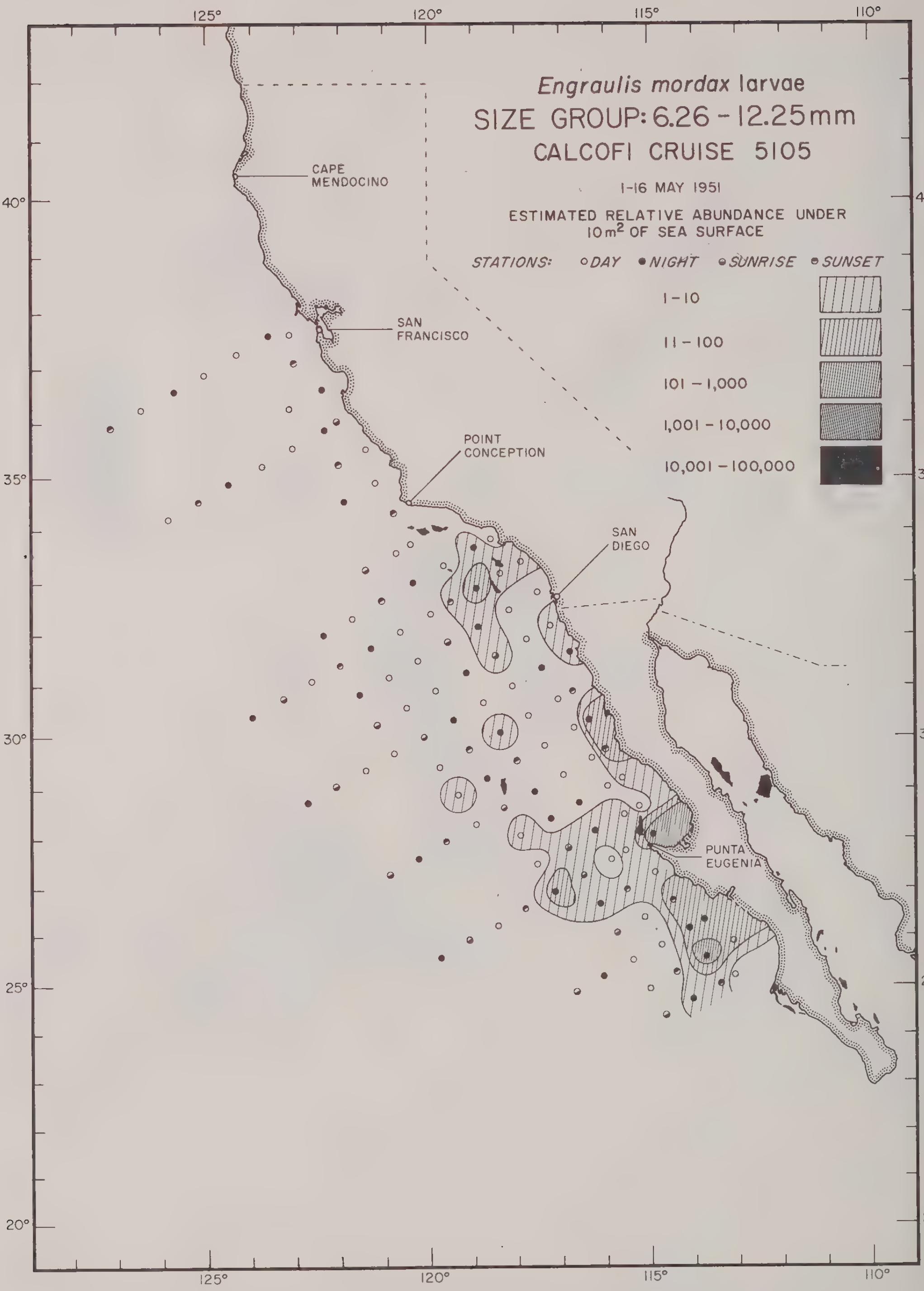
5104


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5104
2-17 APRIL 1951
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

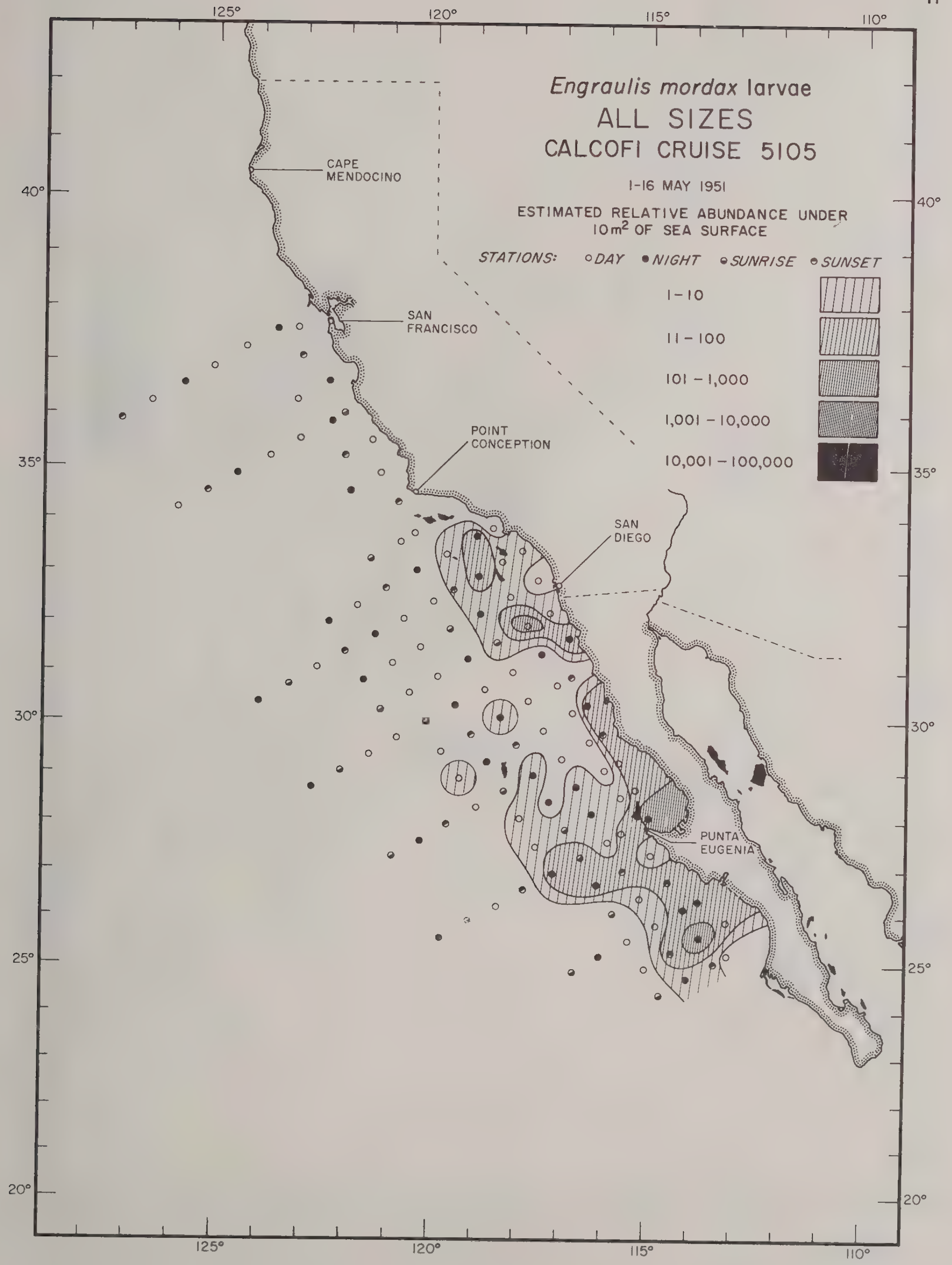
5104


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5105
1-16 MAY 1951
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

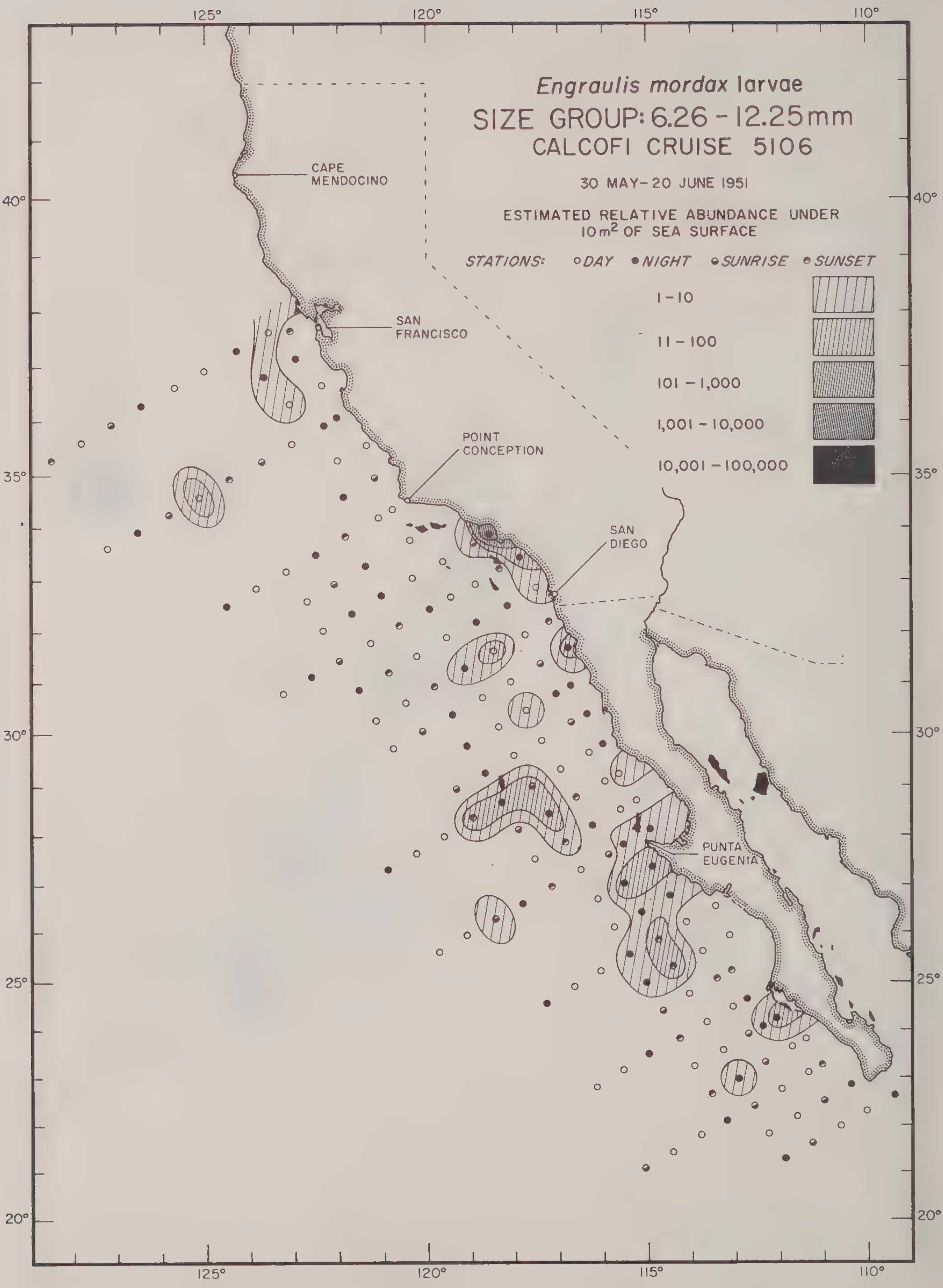
5105


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5105
1-16 MAY 1951
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

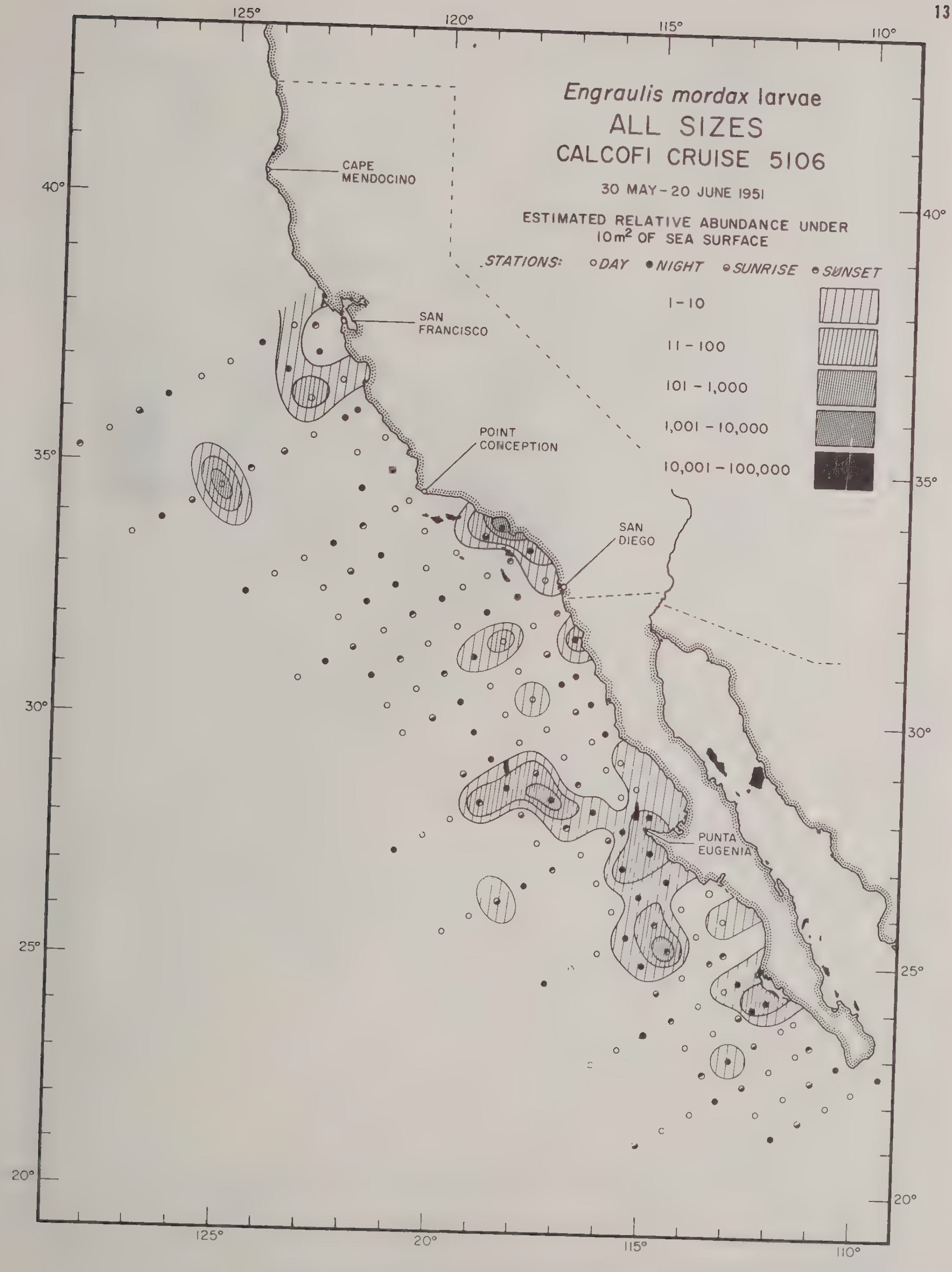
5105


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5106
30 MAY - 20 JUNE 1951
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

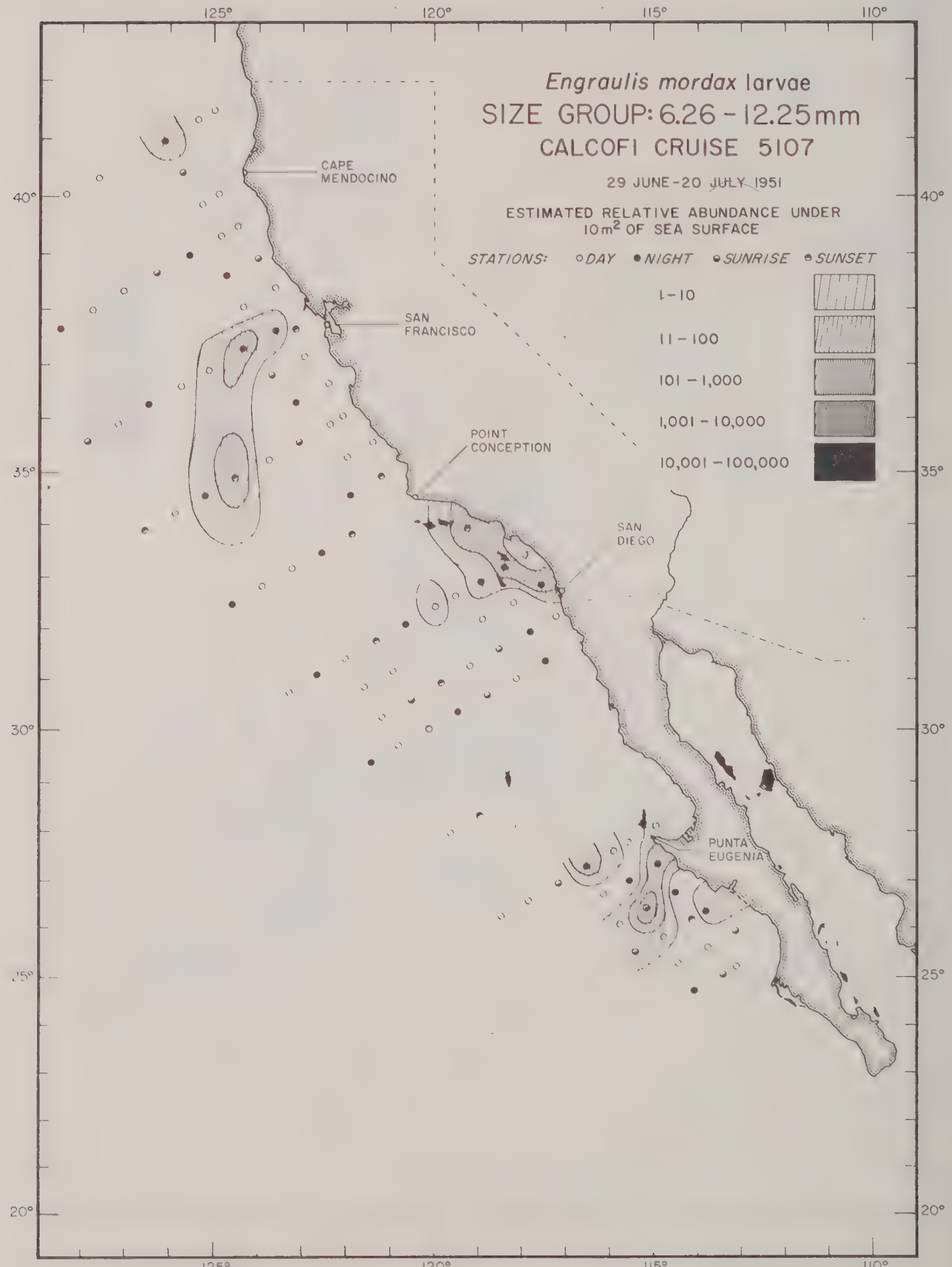
5106


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5106
30 MAY-20 JUNE 1951
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◐SUNRISE ◑SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

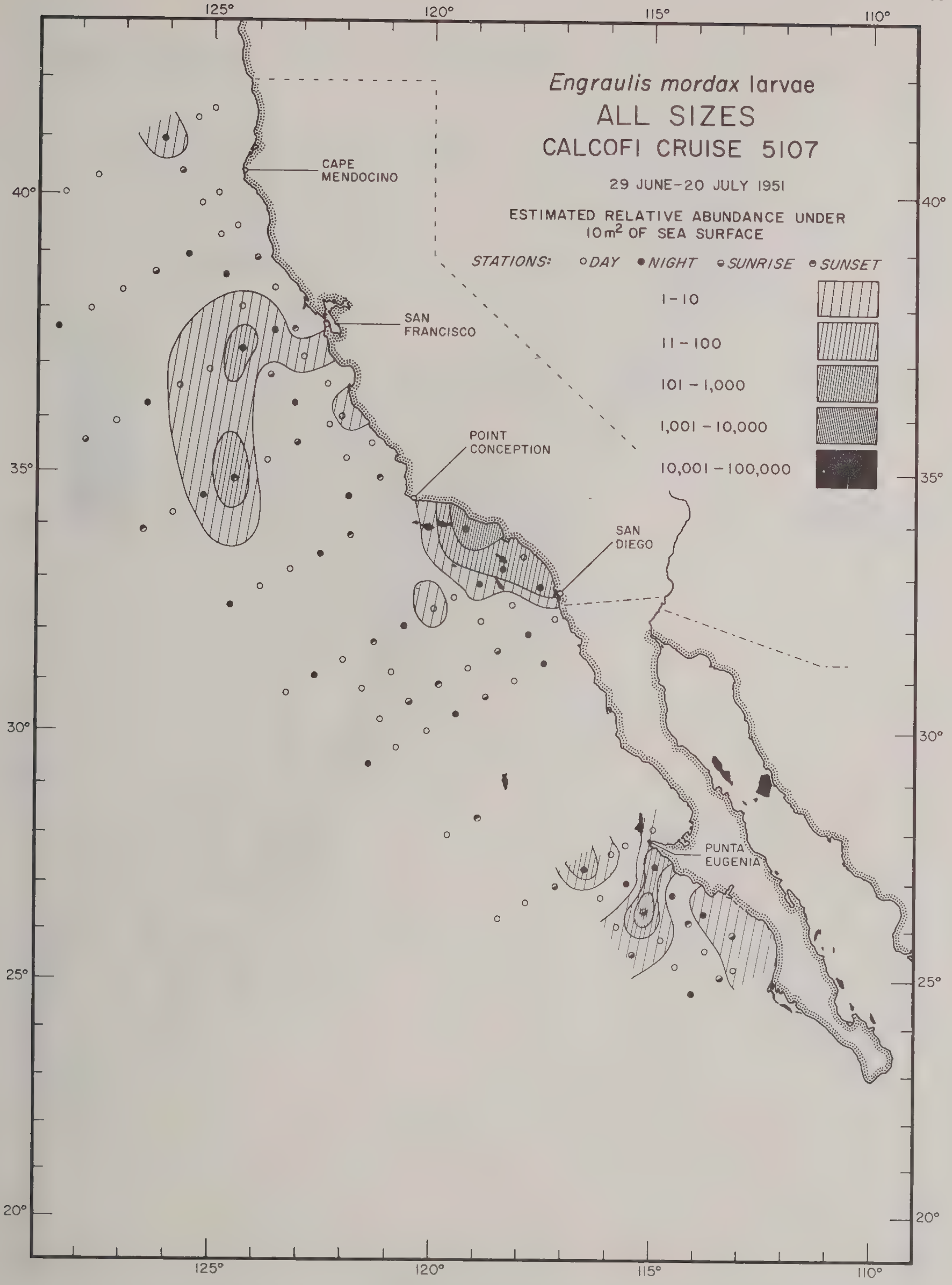
5106


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5107
29 JUNE - 20 ~~JULY~~ 1951
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

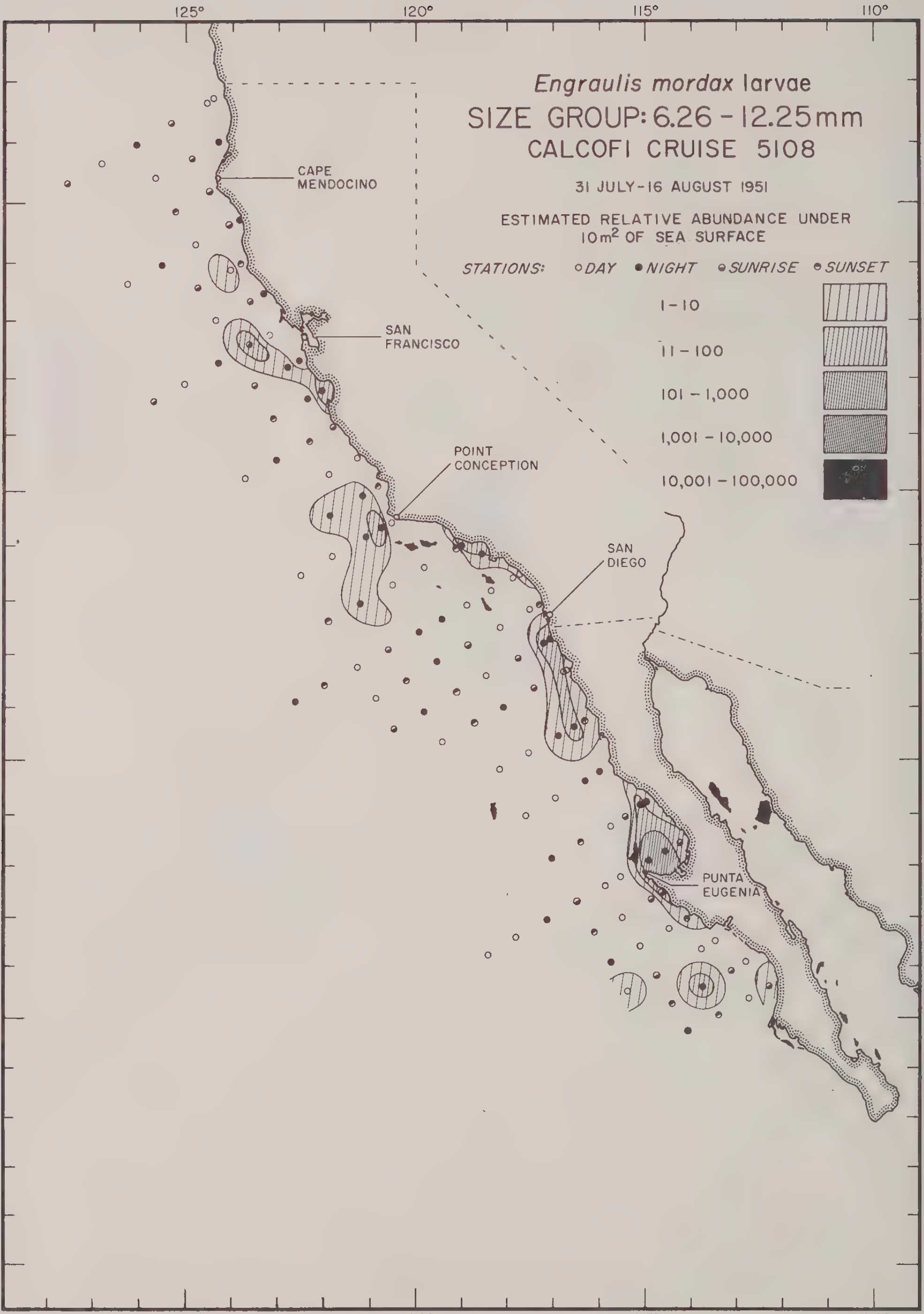
5107


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5107
29 JUNE-20 JULY 1951
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

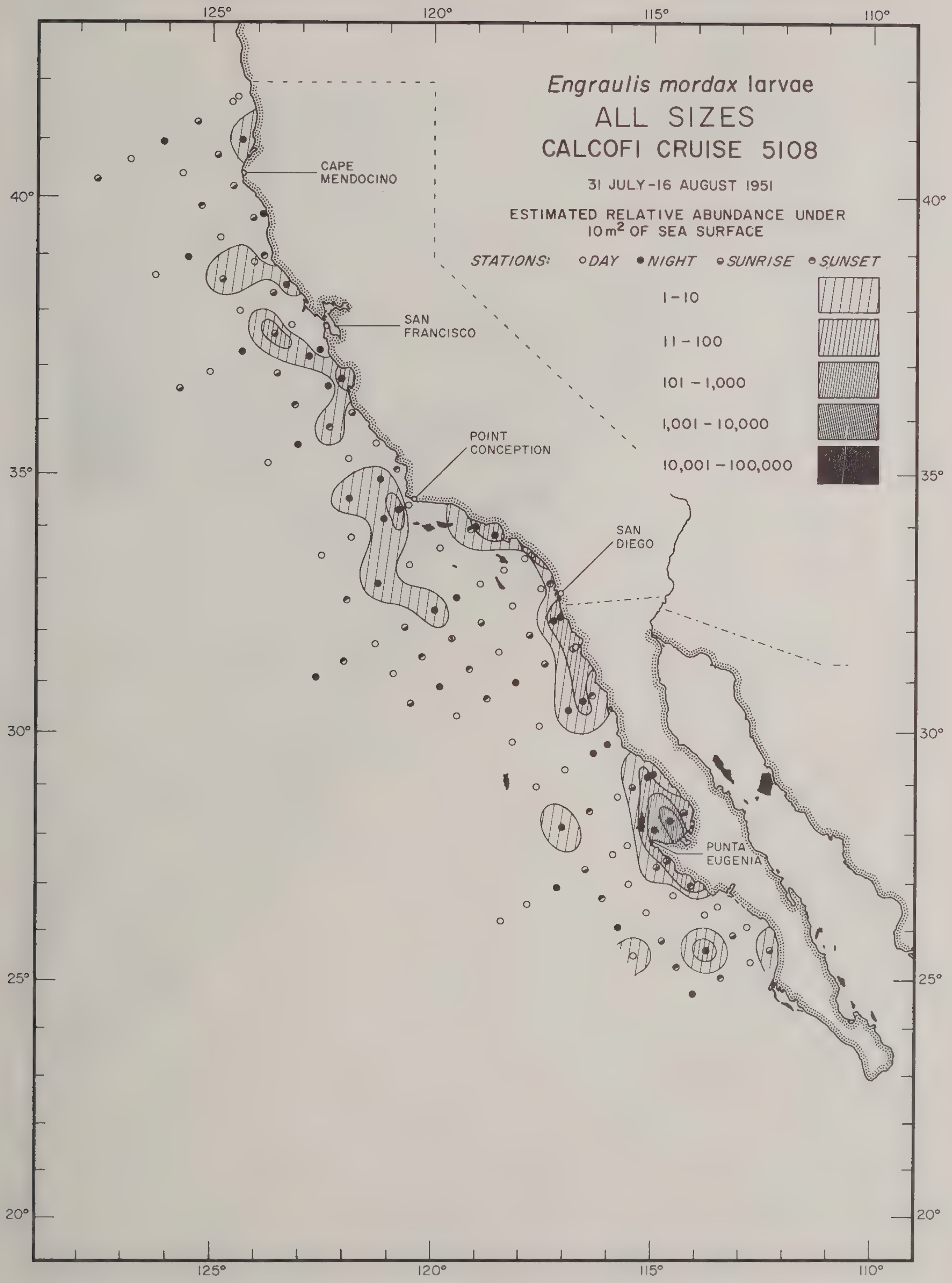
5107


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5108
31 JULY-16 AUGUST 1951
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

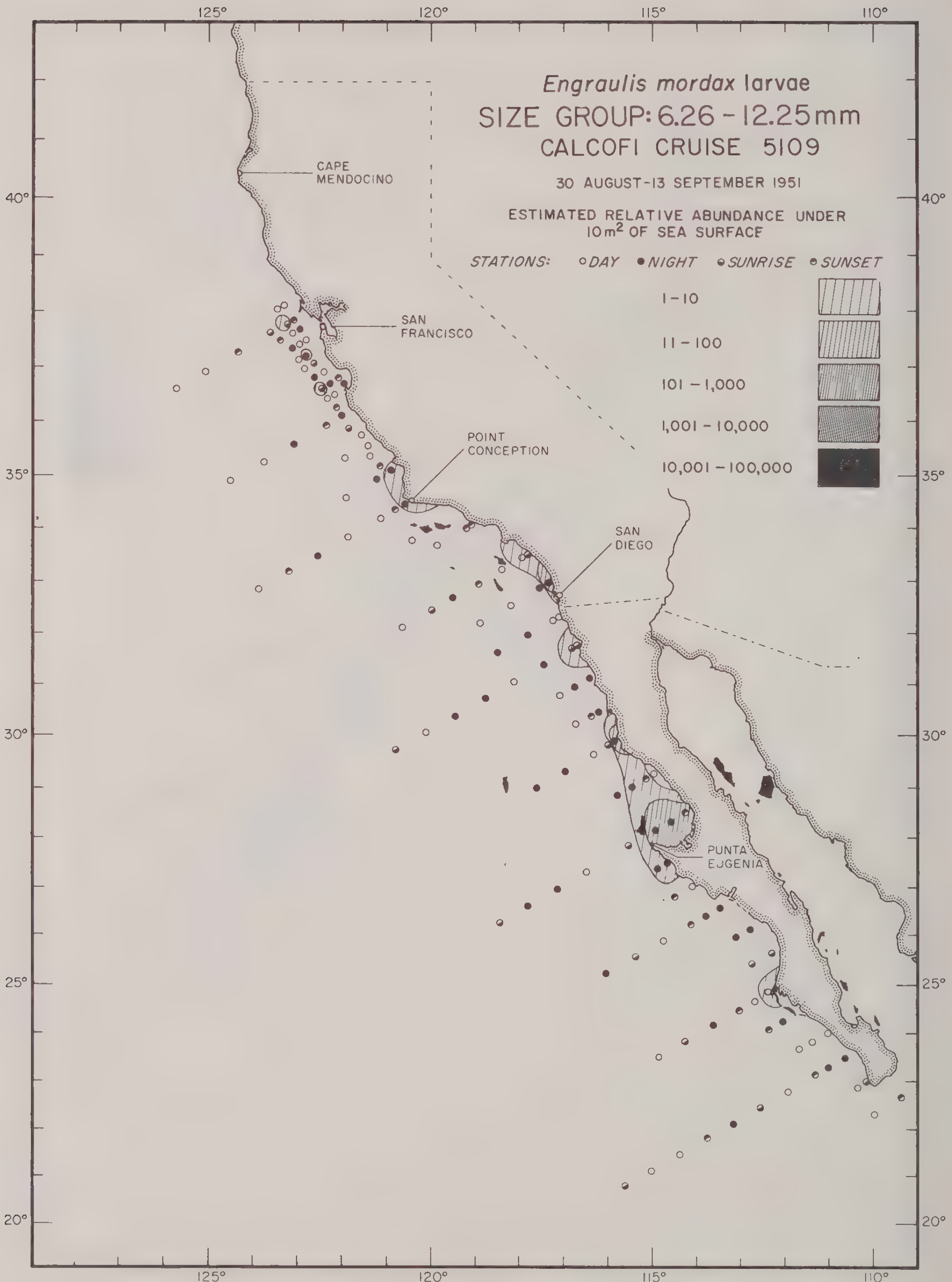
5108


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5108
31 JULY-16 AUGUST 1951
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

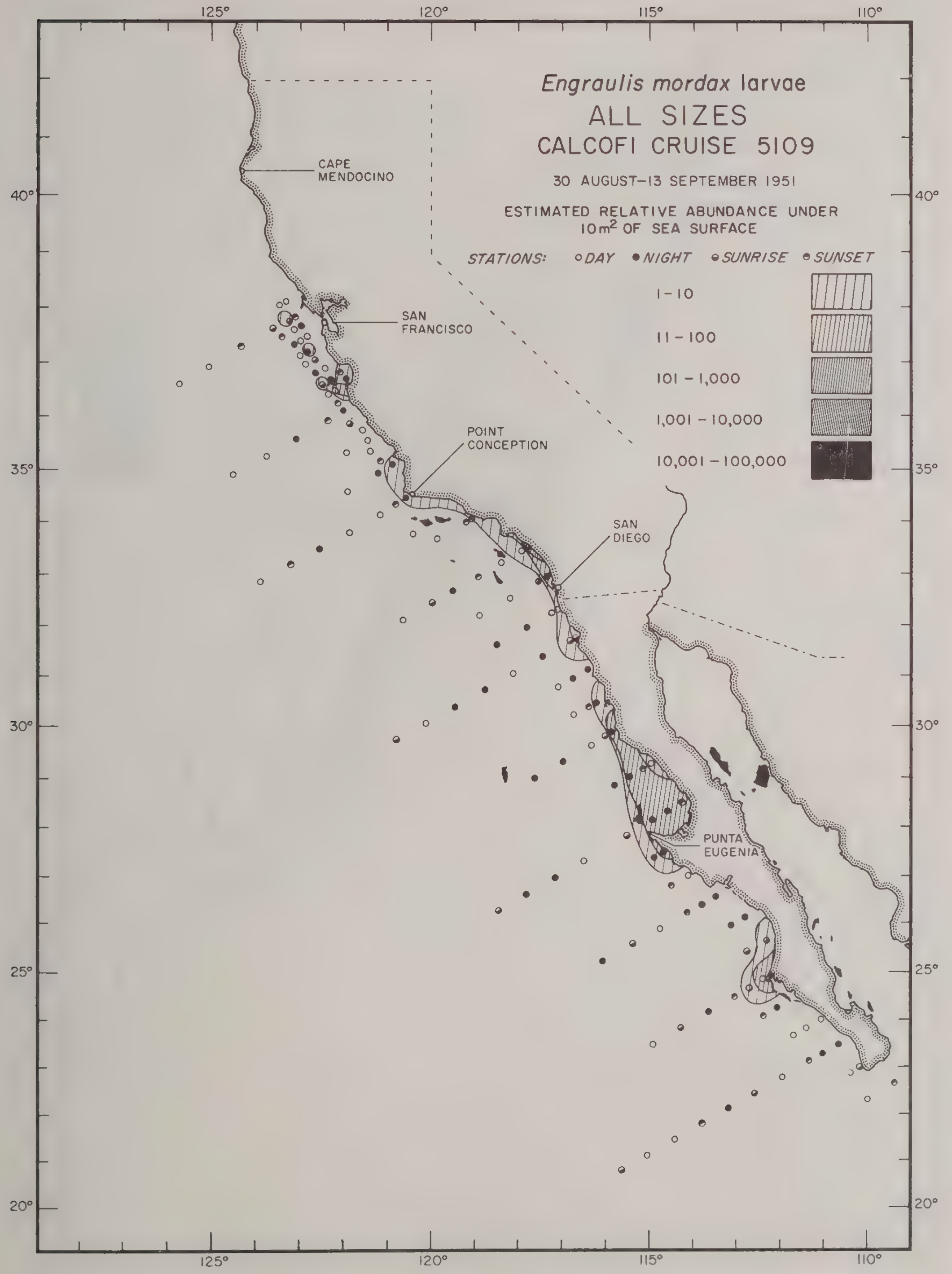
5108


125°
120°
115°
110°
Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5109
30 AUGUST-13 SEPTEMBER 1951
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
40°
35°
30°
25°
20°

Engraulis mordax larvae

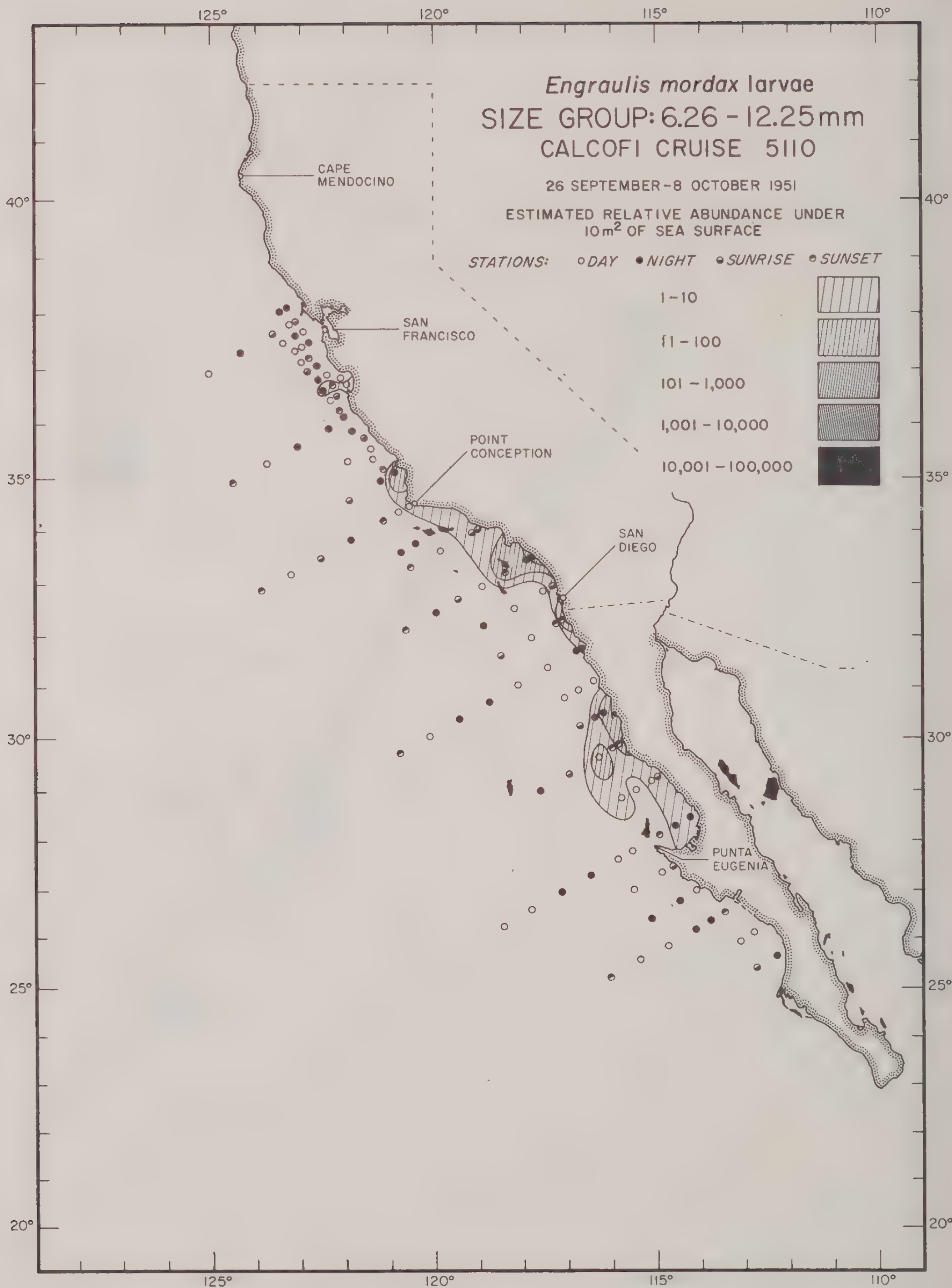
Size Group: 6.26-12.25mm

5109


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5109
30 AUGUST–13 SEPTEMBER 1951
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1–10
11–100
101–1,000
1,001–10,000
10,001–100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

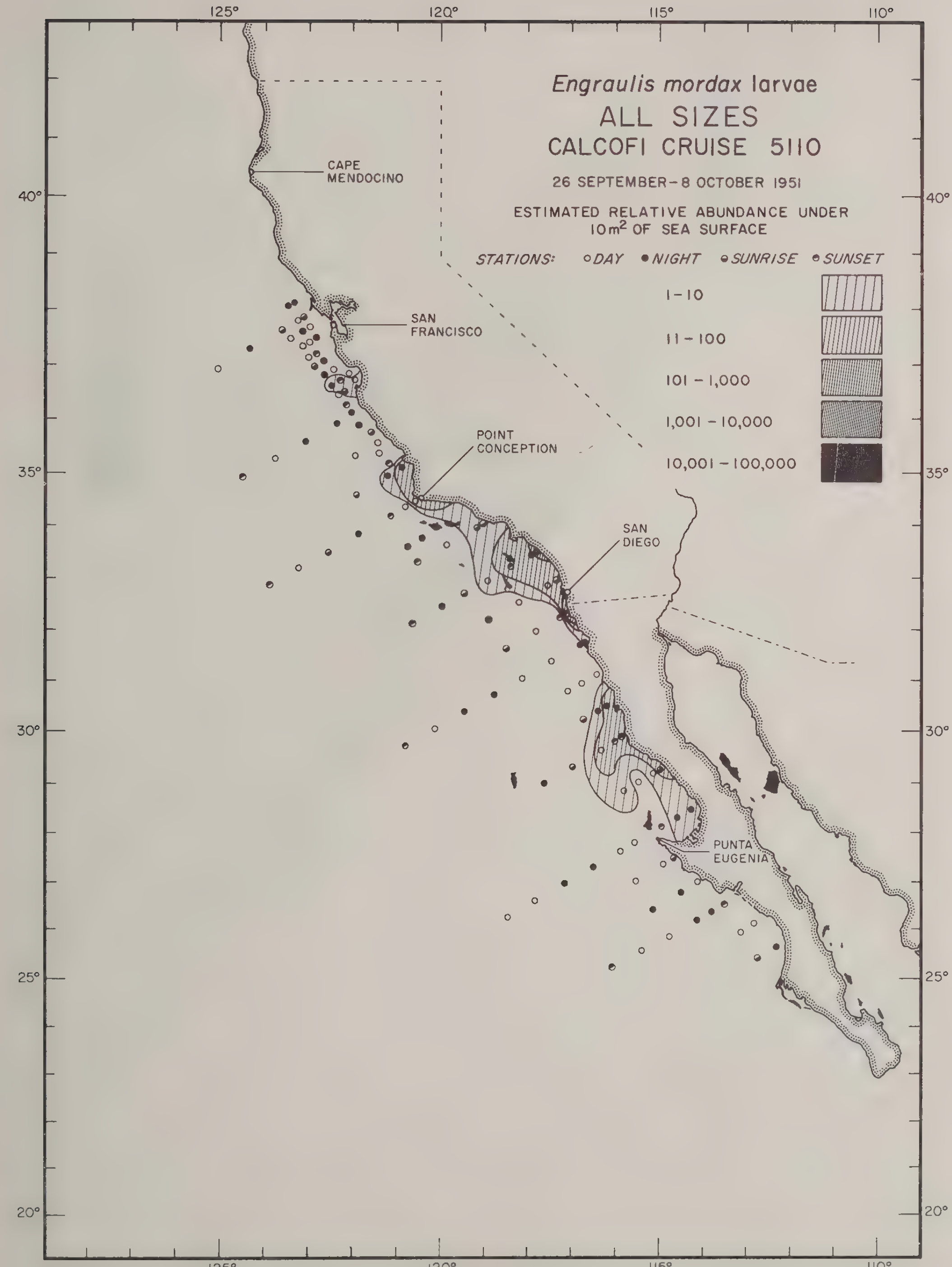
All Sizes
5109


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5110
26 SEPTEMBER - 8 OCTOBER 1951
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ *DAY* ● *NIGHT* *SUNRISE* *SUNSET*
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

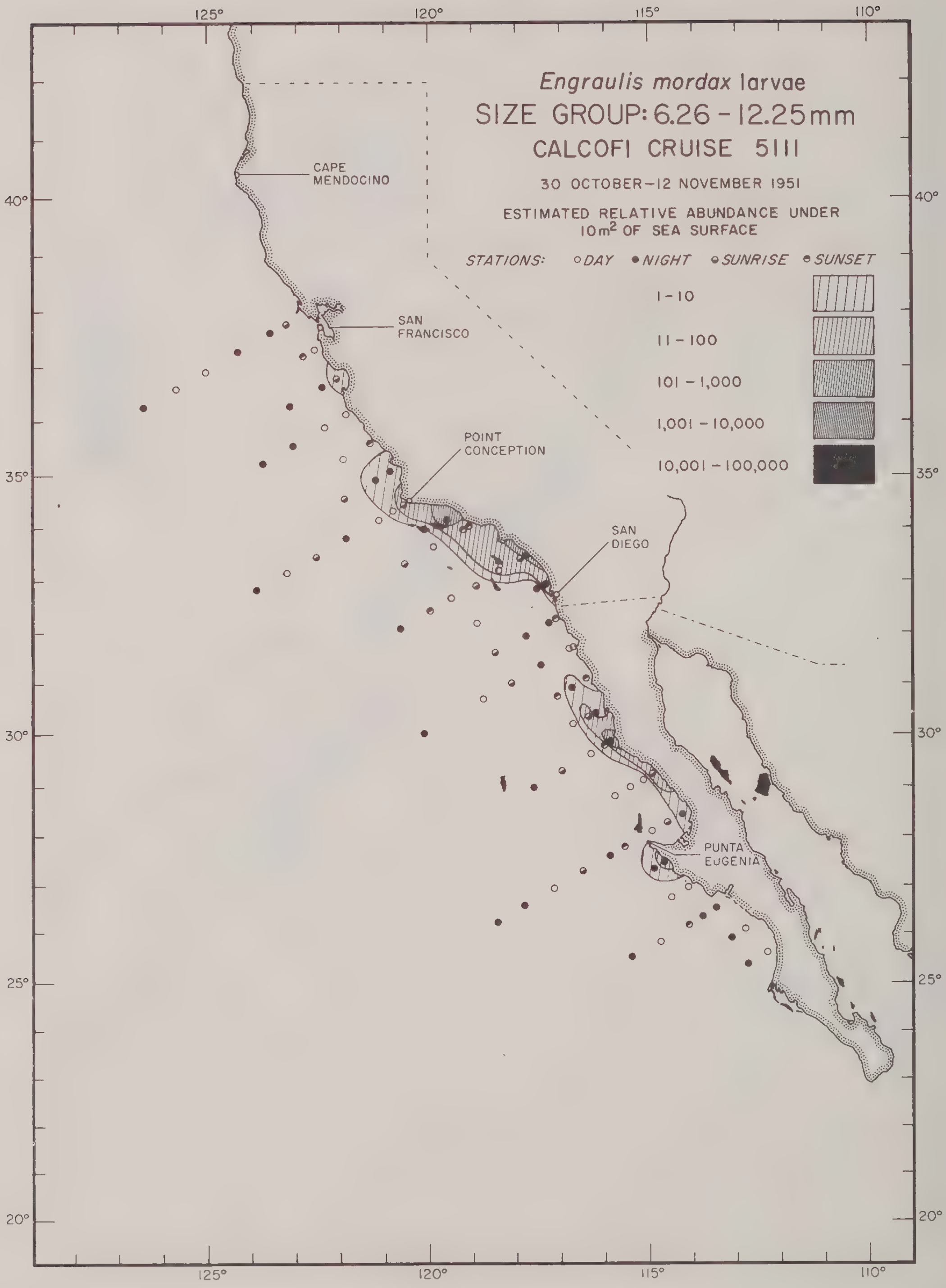
5110


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5110
26 SEPTEMBER – 8 OCTOBER 1951
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

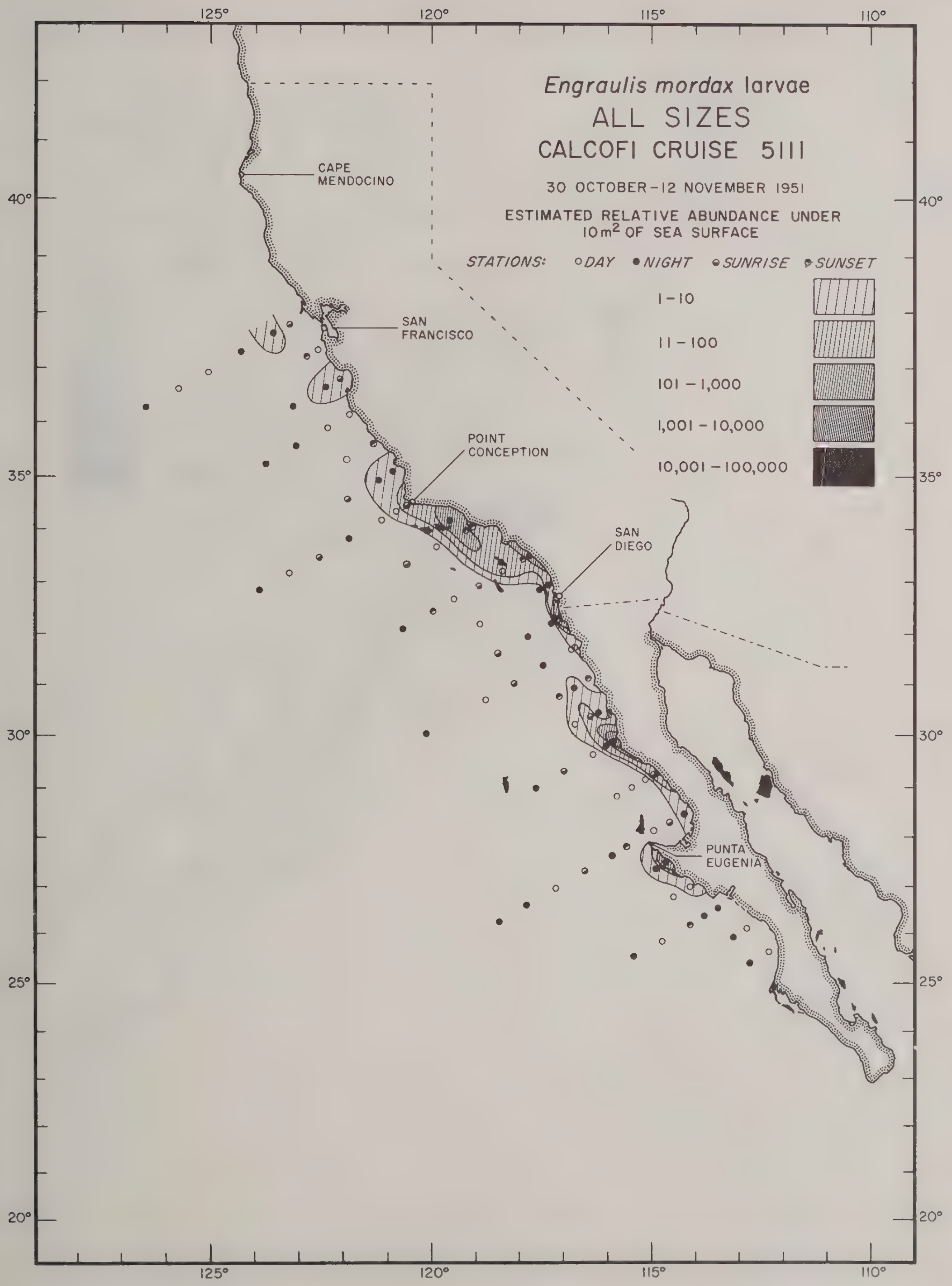
5110


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5111
30 OCTOBER-12 NOVEMBER 1951
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

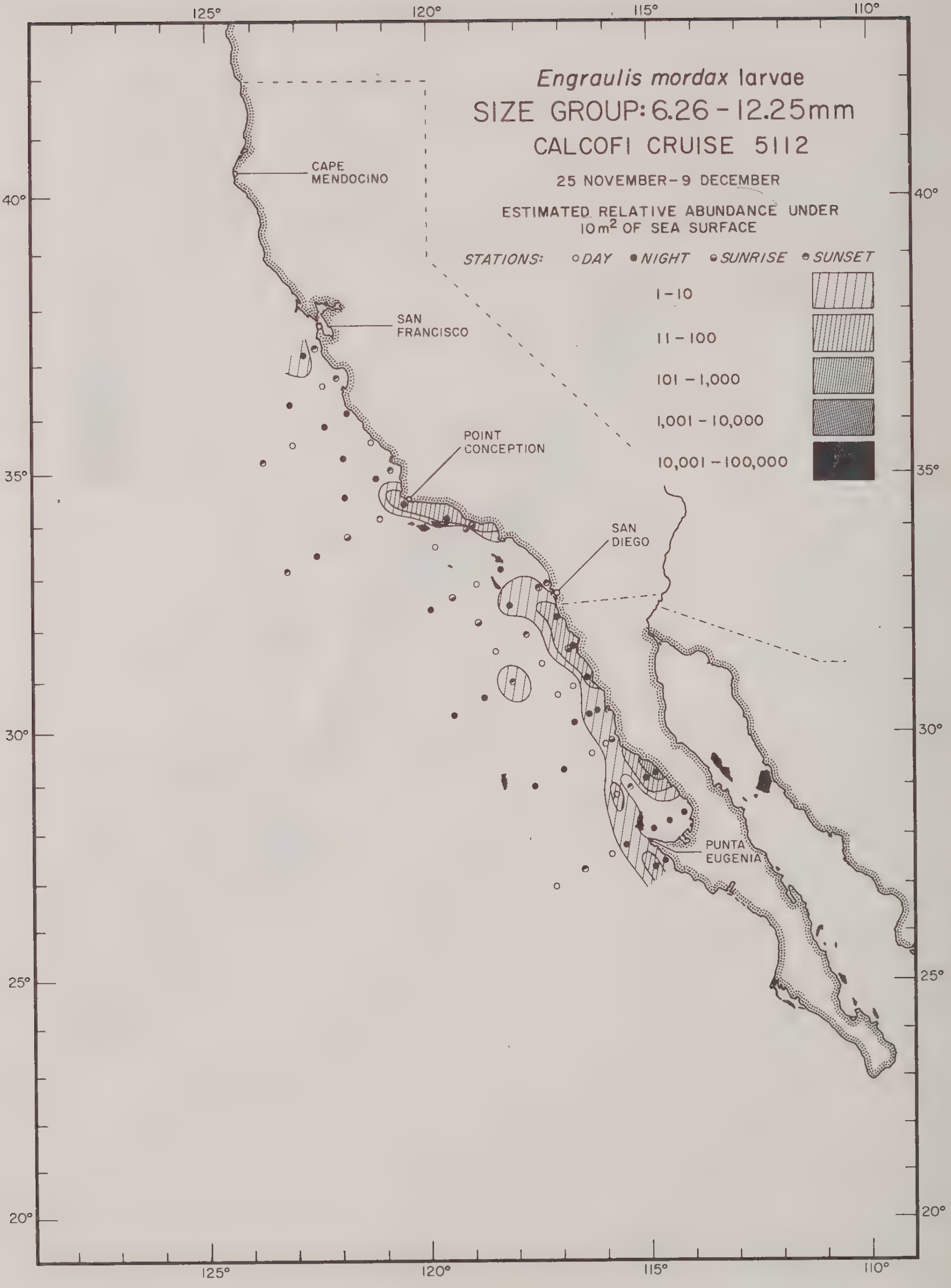
5111


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5111
30 OCTOBER-12 NOVEMBER 1951
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

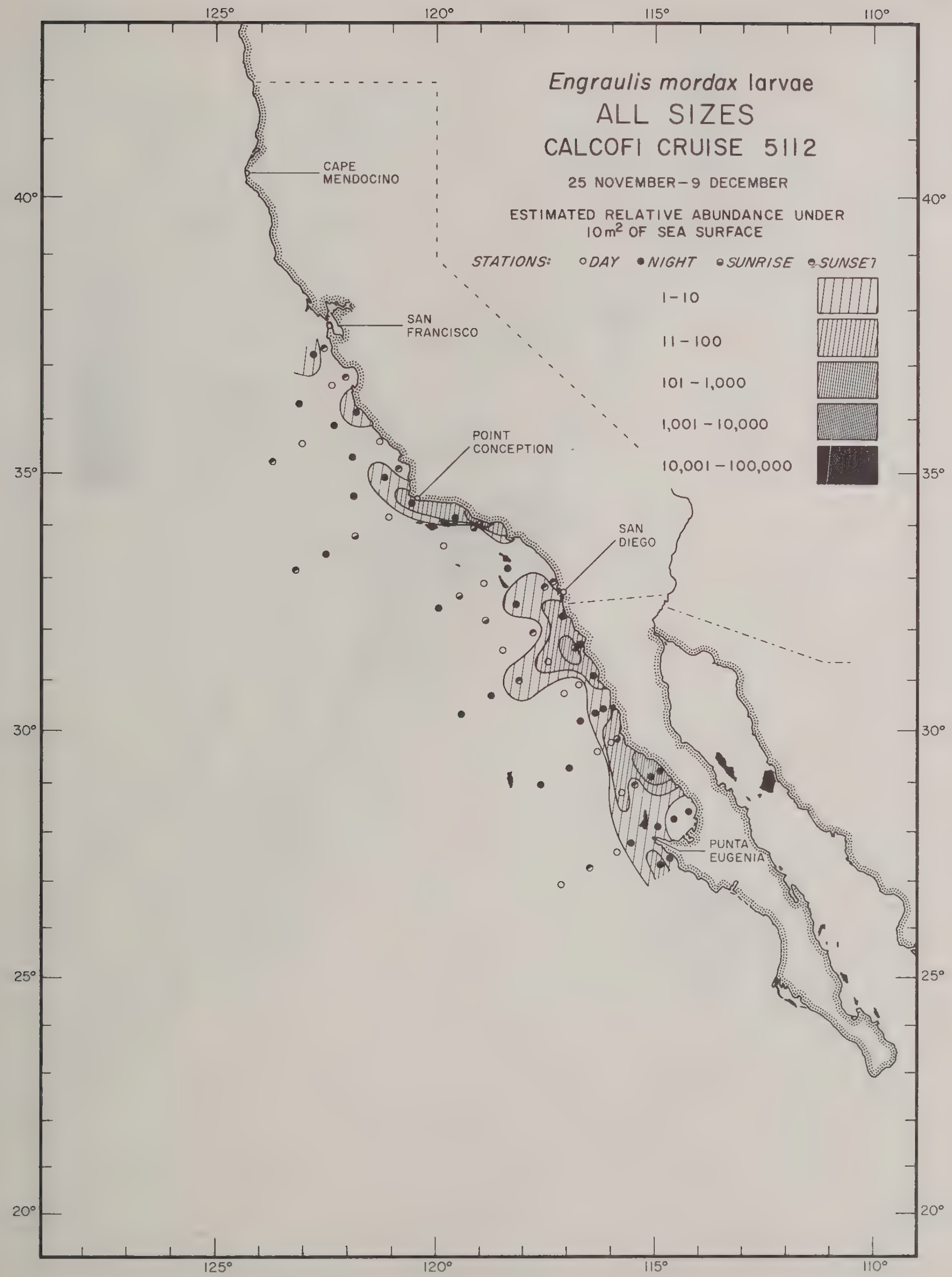
5111


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5112
25 NOVEMBER - 9 DECEMBER
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

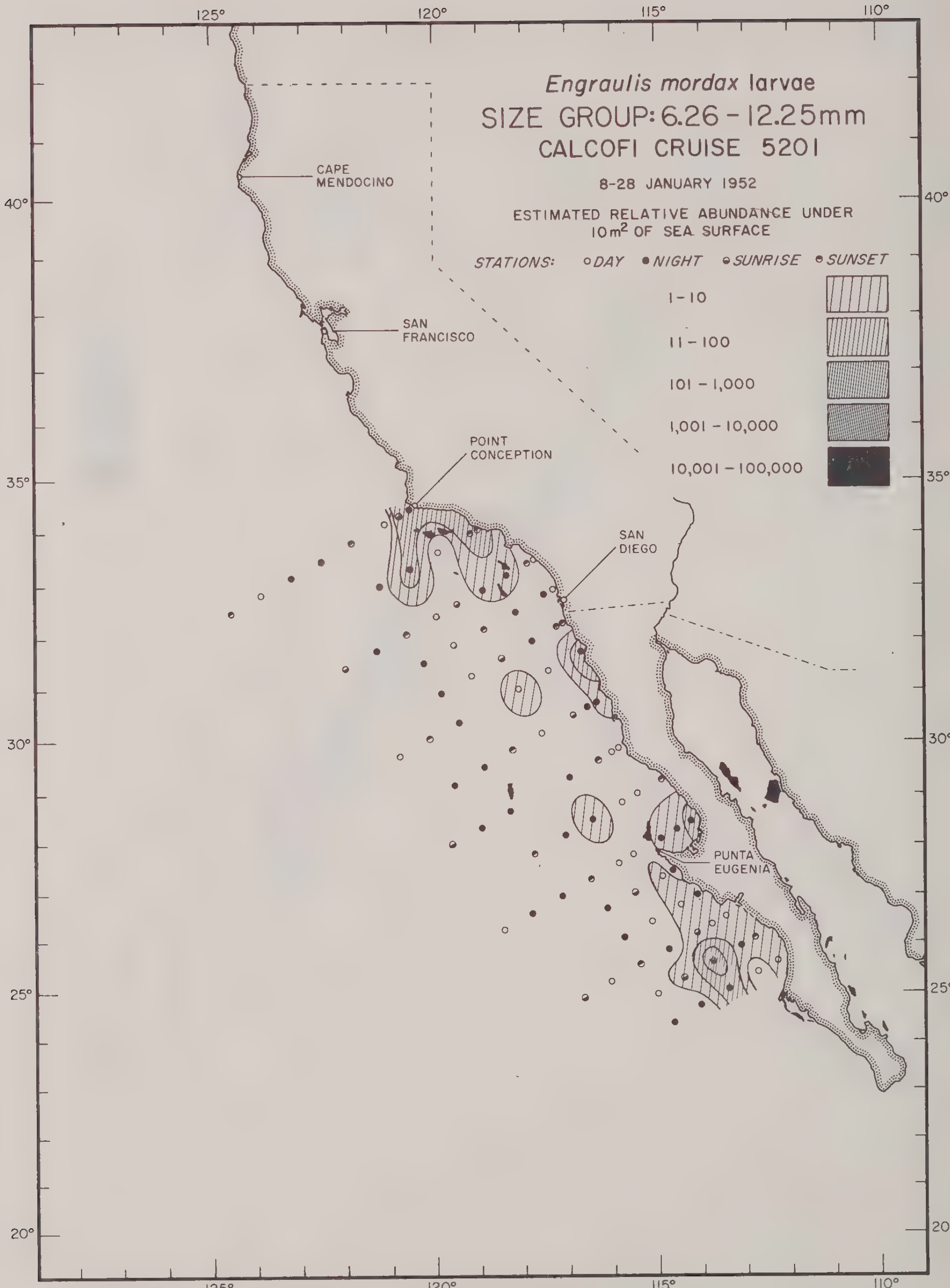
5112


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5112
25 NOVEMBER–9 DECEMBER
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

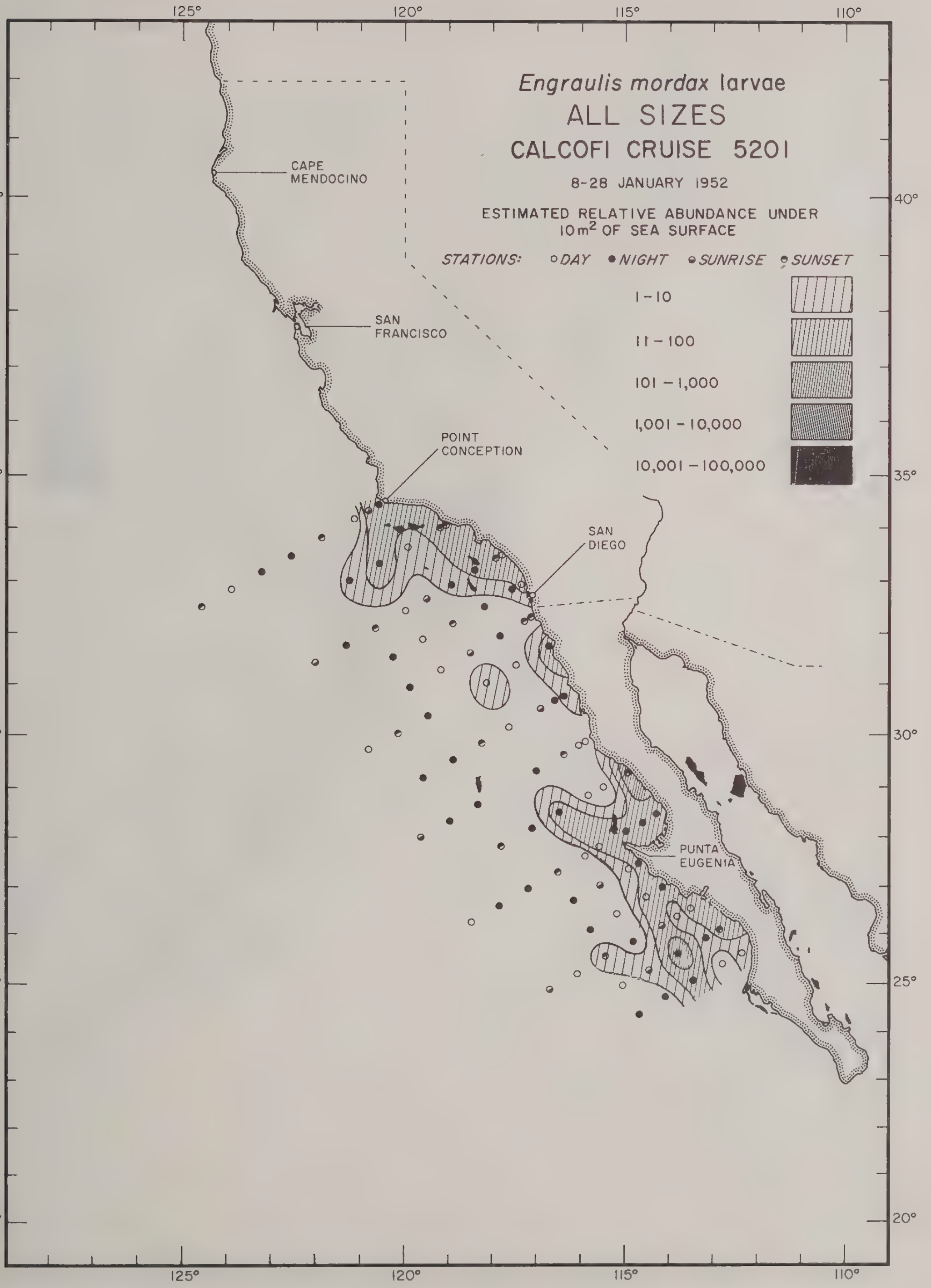
5112


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5201
8-28 JANUARY 1952
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

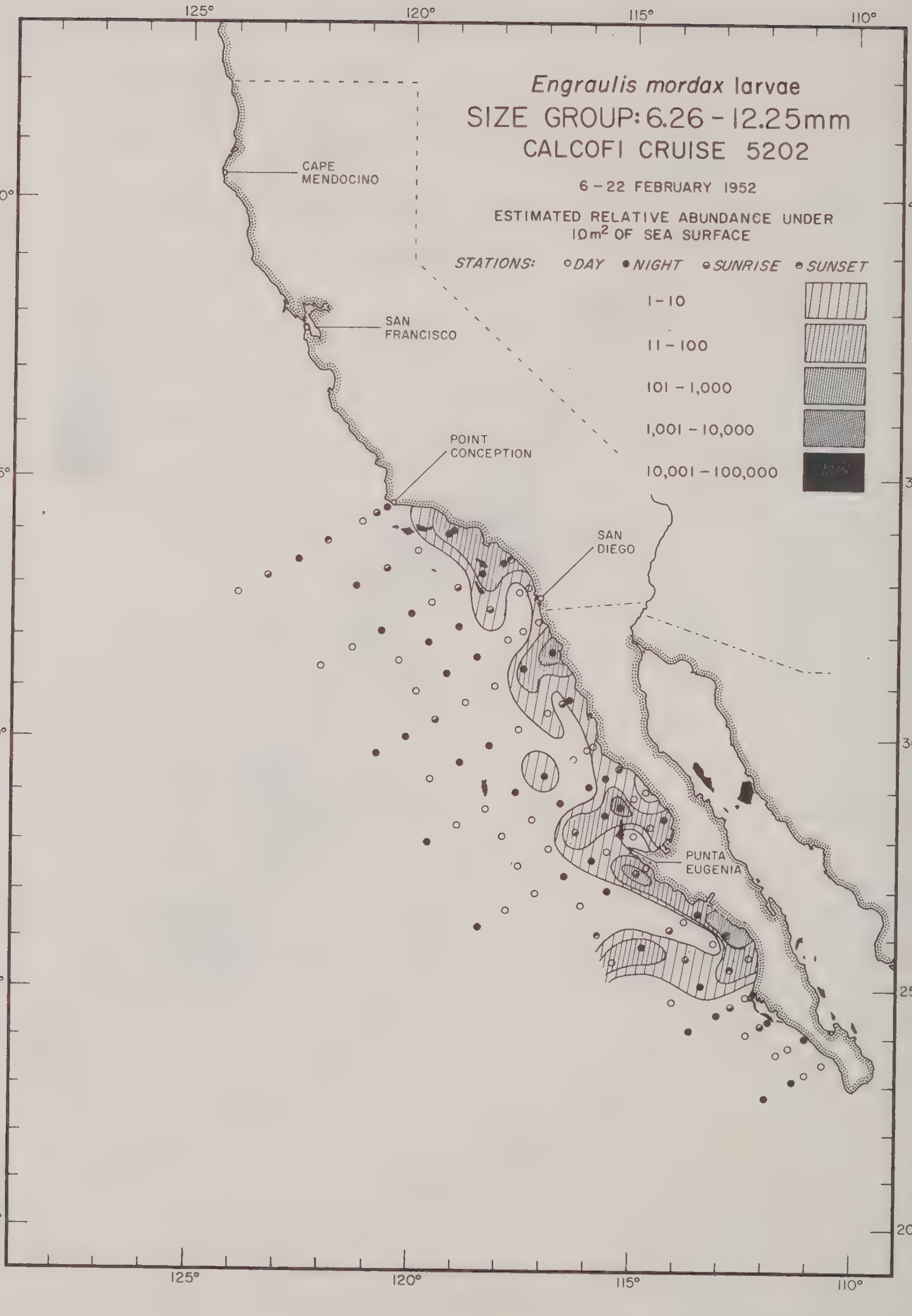
5201


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5201
8-28 JANUARY 1952
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

All Sizes

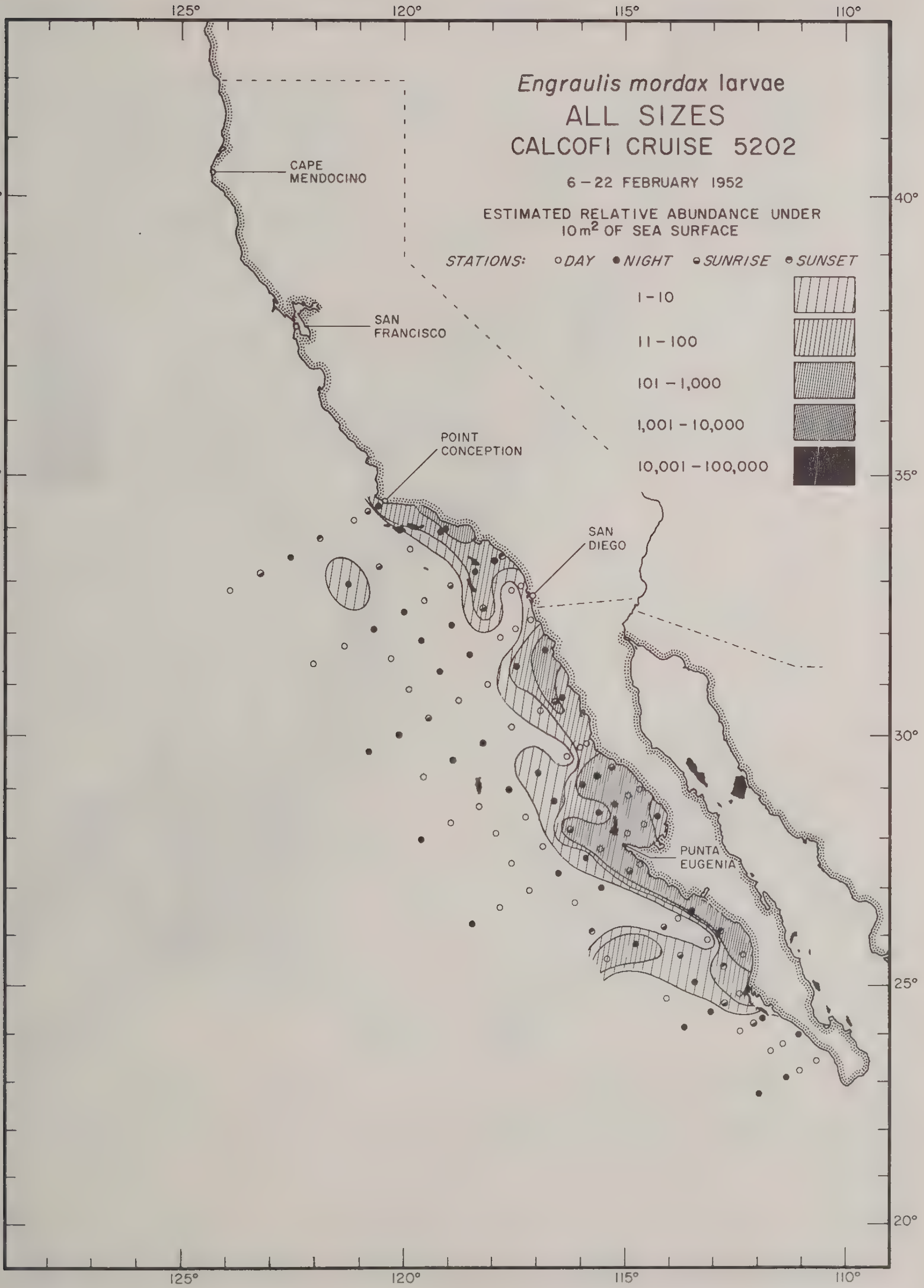
5201


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5202
6 - 22 FEBRUARY 1952
ESTIMATED RELATIVE ABUNDANCE UNDER 1.0m² OF SEA SURFACE
STATIONS: ○ *DAY* ● *NIGHT* ◐ *SUNRISE* ◑ *SUNSET*
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

5202

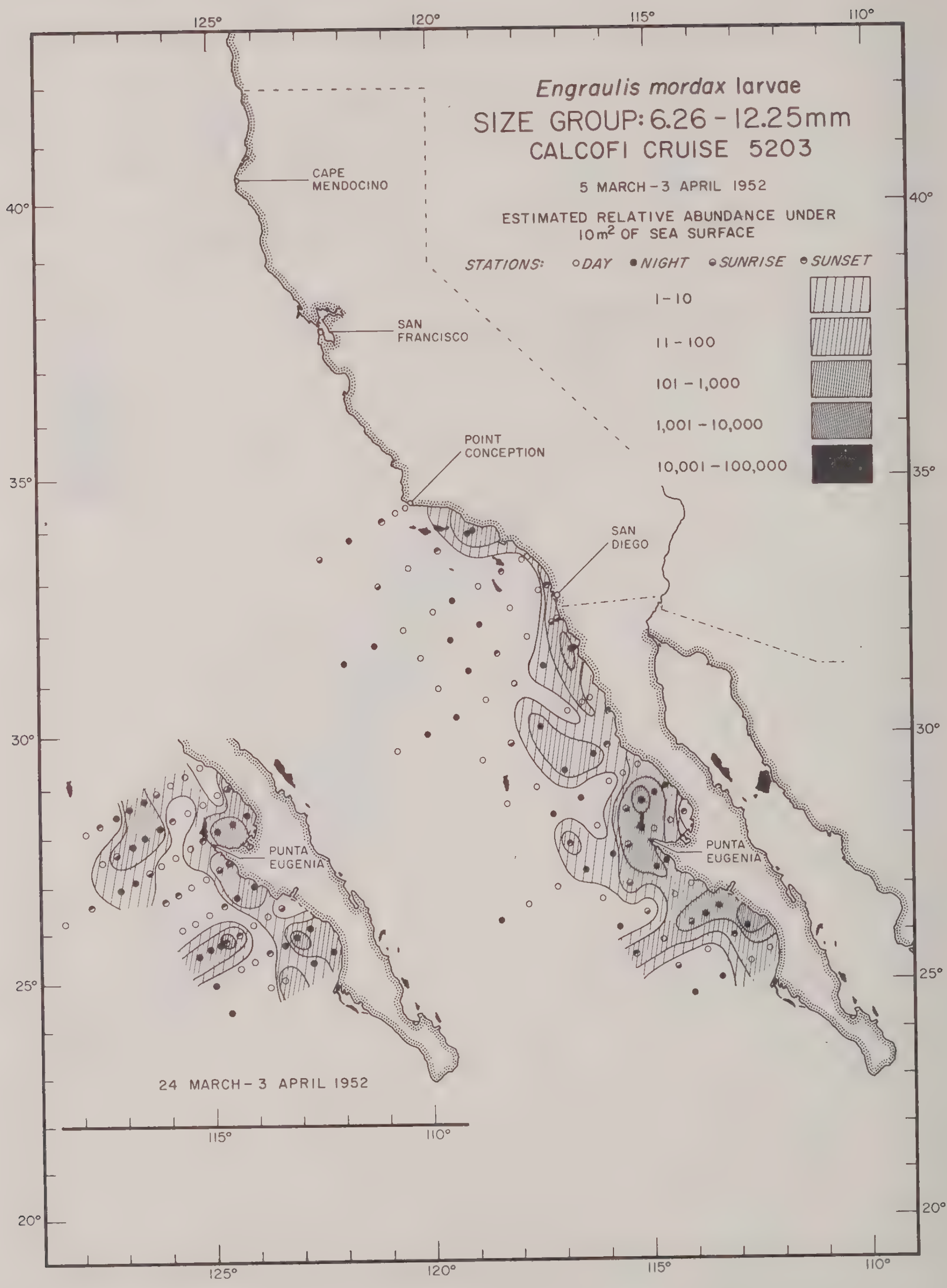


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5202
6 – 22 FEBRUARY 1952
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

All Sizes

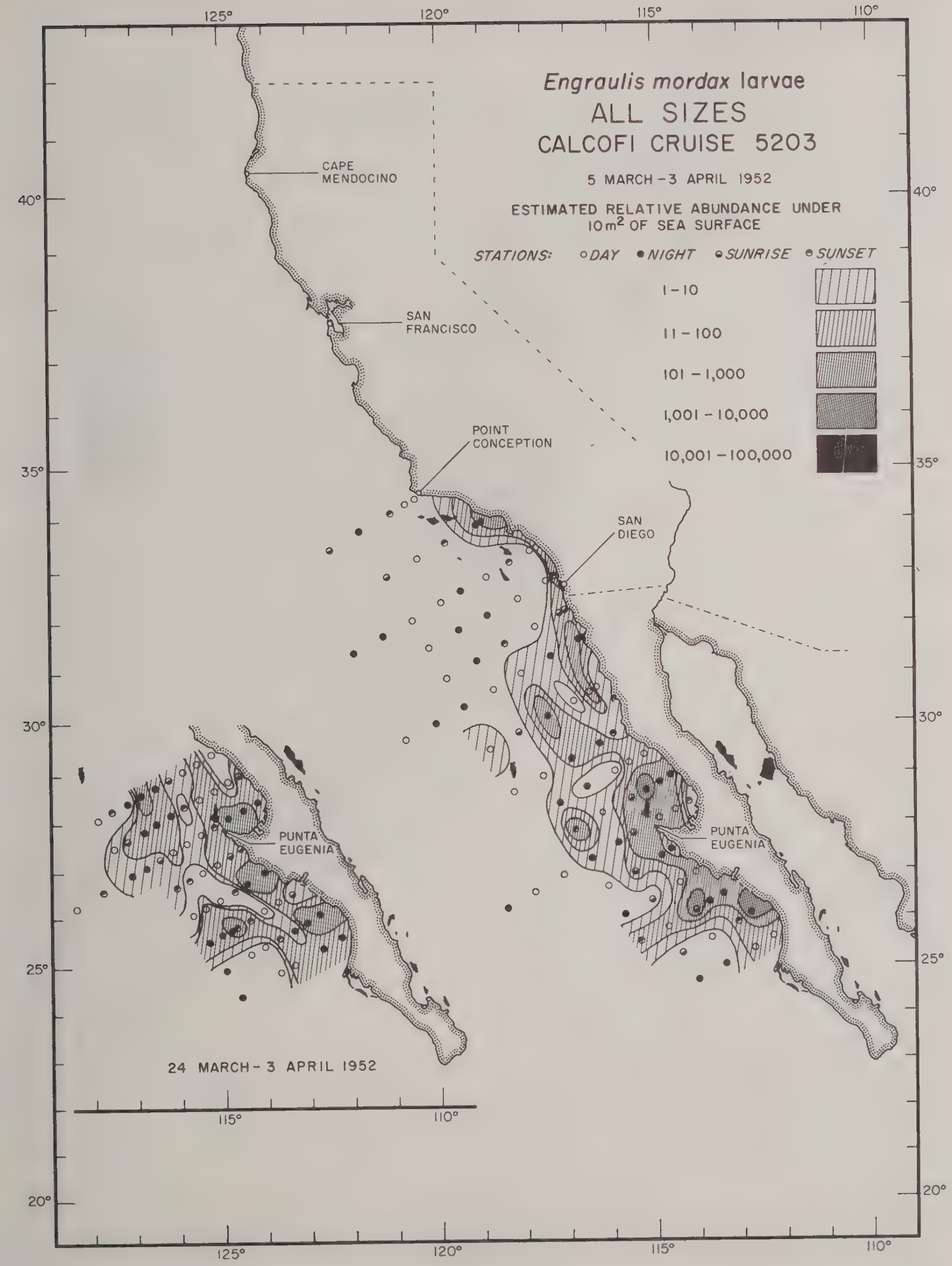
5202


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5203
5 MARCH - 3 APRIL 1952
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
PUNTA EUGENIA
24 MARCH - 3 APRIL 1952
125°
120°
115°
110°
40°
35°
30°
25°
20°
115°
110°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

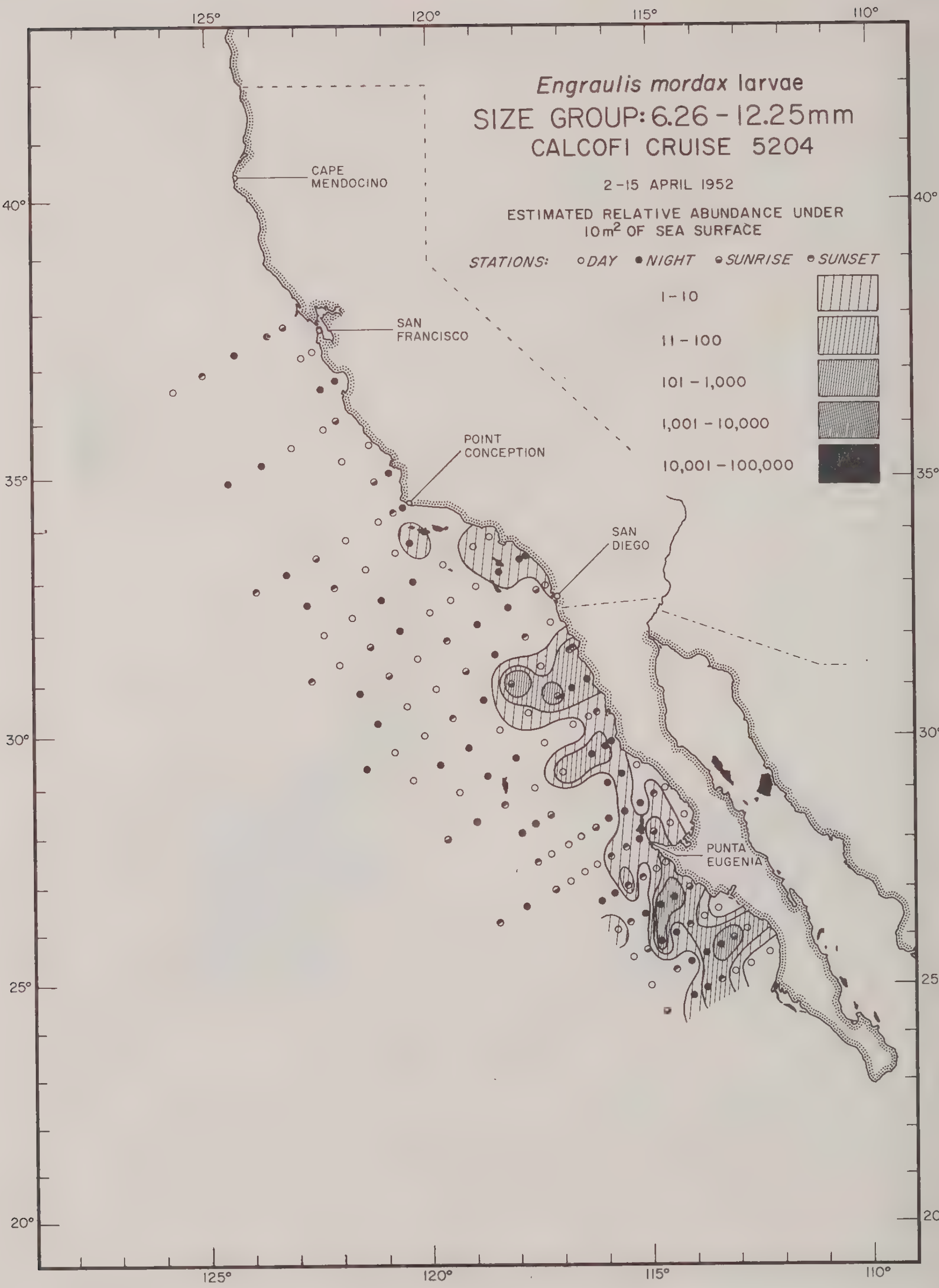
5203


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5203
5 MARCH - 3 APRIL 1952
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
PUNTA EUGENIA
24 MARCH - 3 APRIL 1952
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

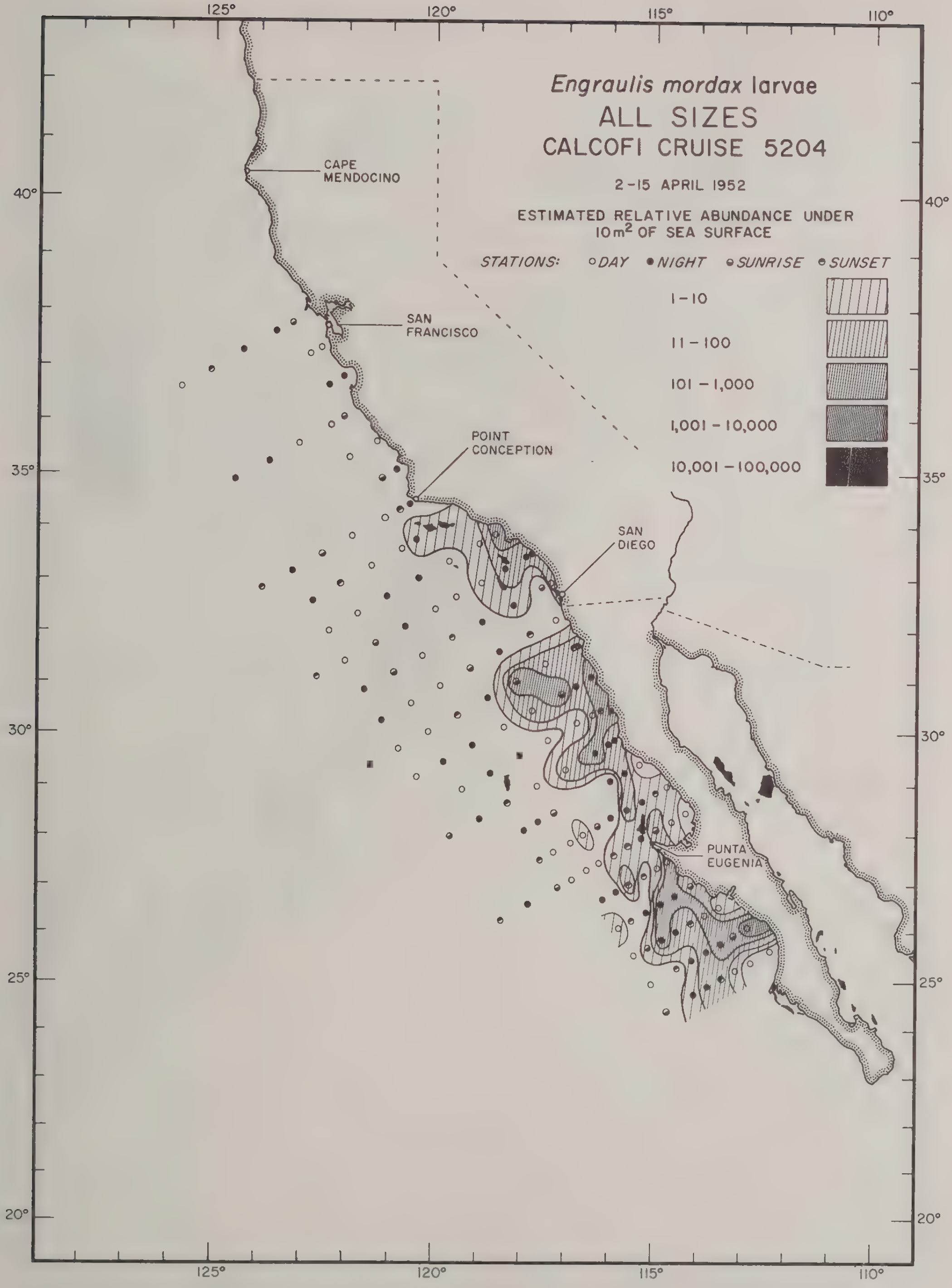
5203


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5204
2-15 APRIL 1952
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○ *DAY* ● *NIGHT* ◉ *SUNRISE* ◉ *SUNSET*
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

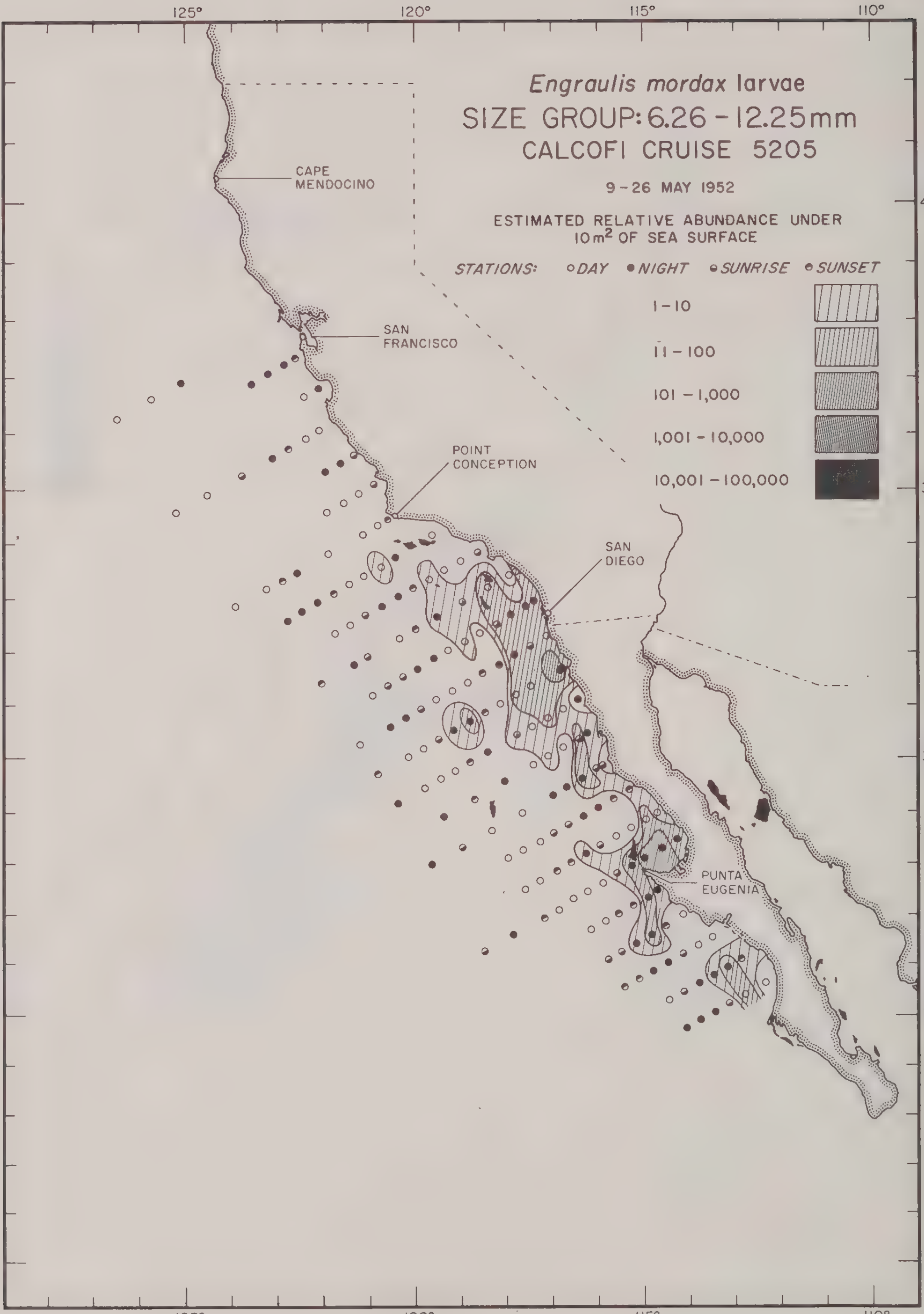
5204


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5204
2-15 APRIL 1952
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

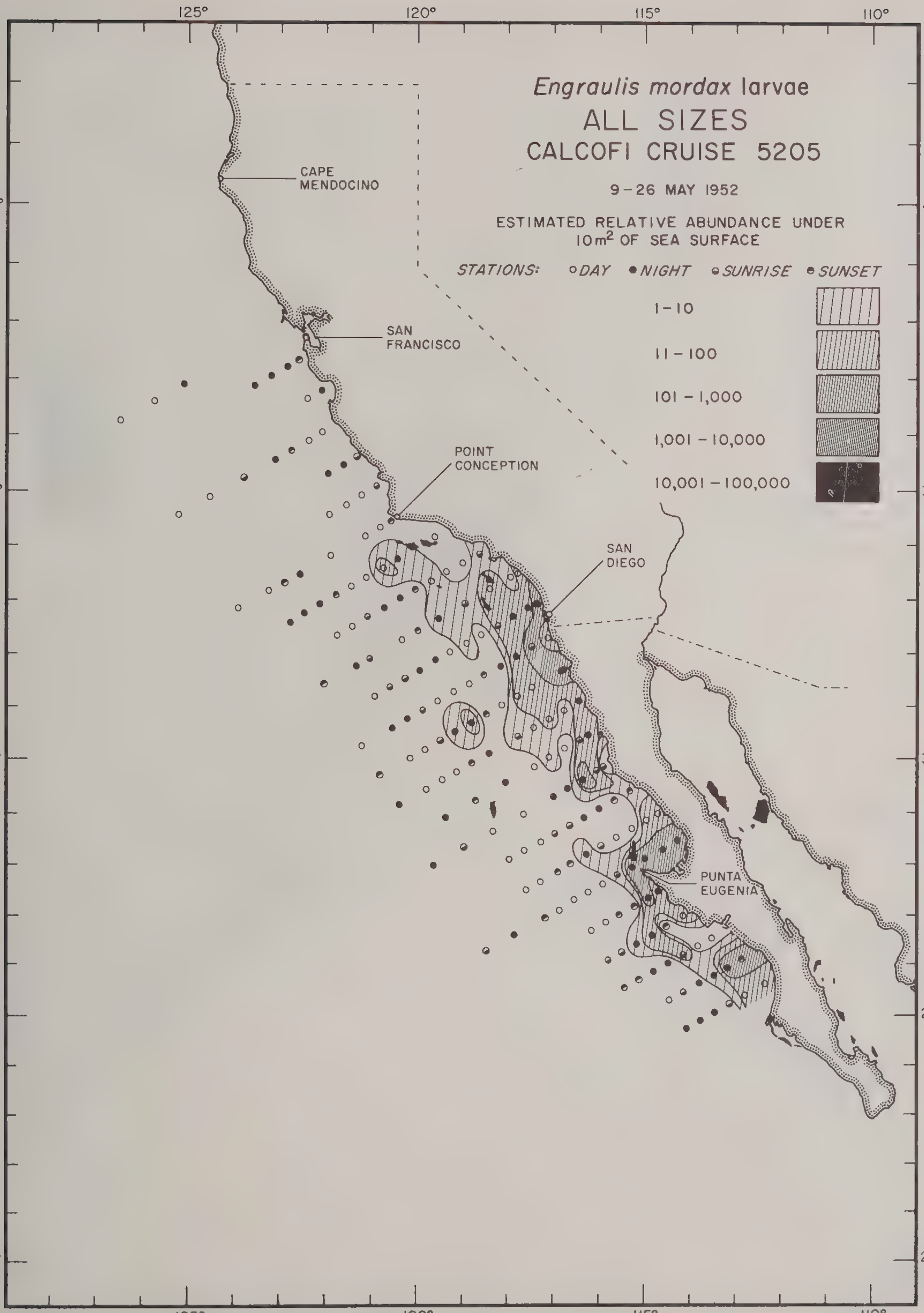
5204


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5205
9-26 MAY 1952
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

Size Group: 6.26-12.25mm

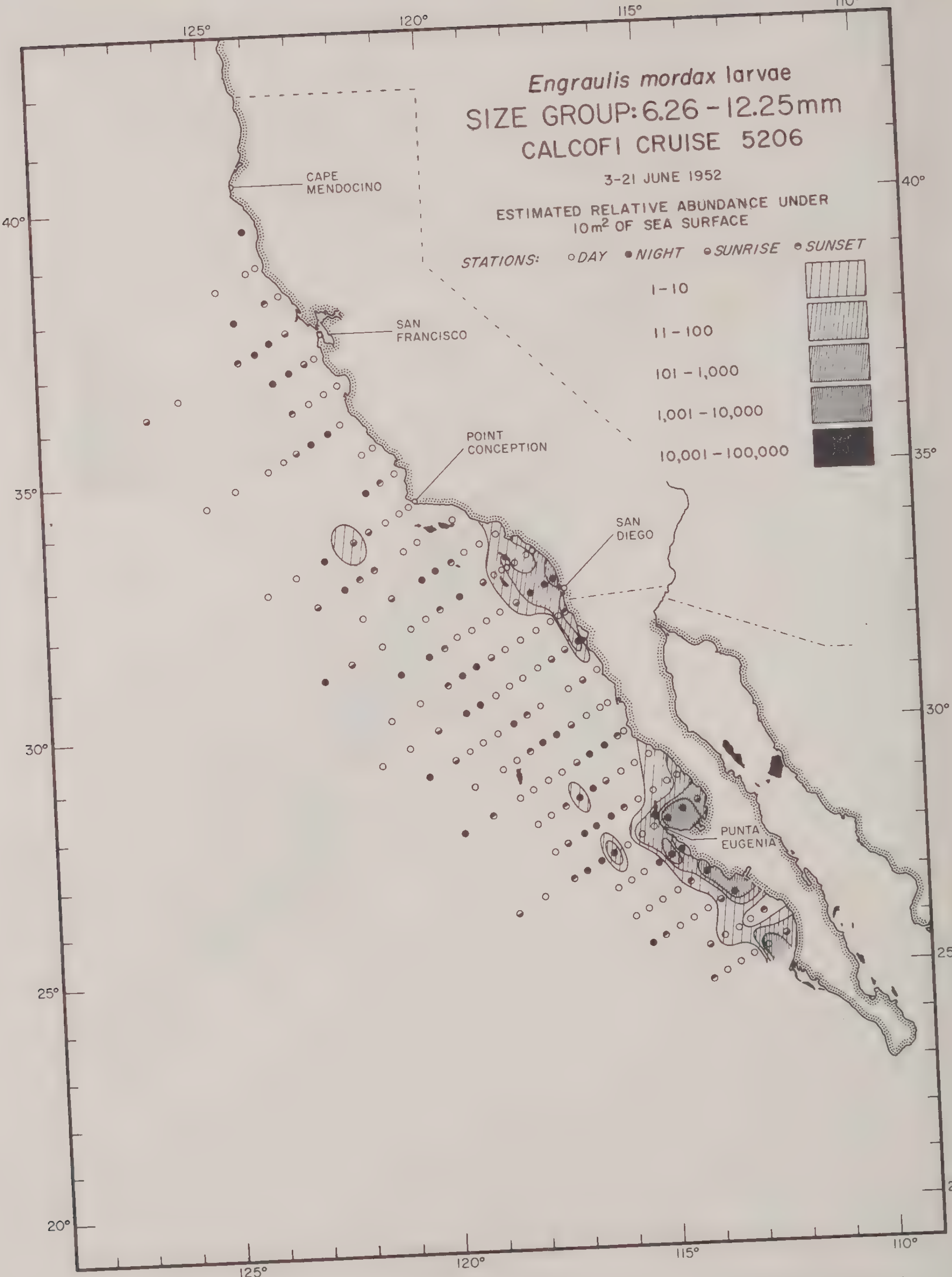
5205


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5205
9-26 MAY 1952
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

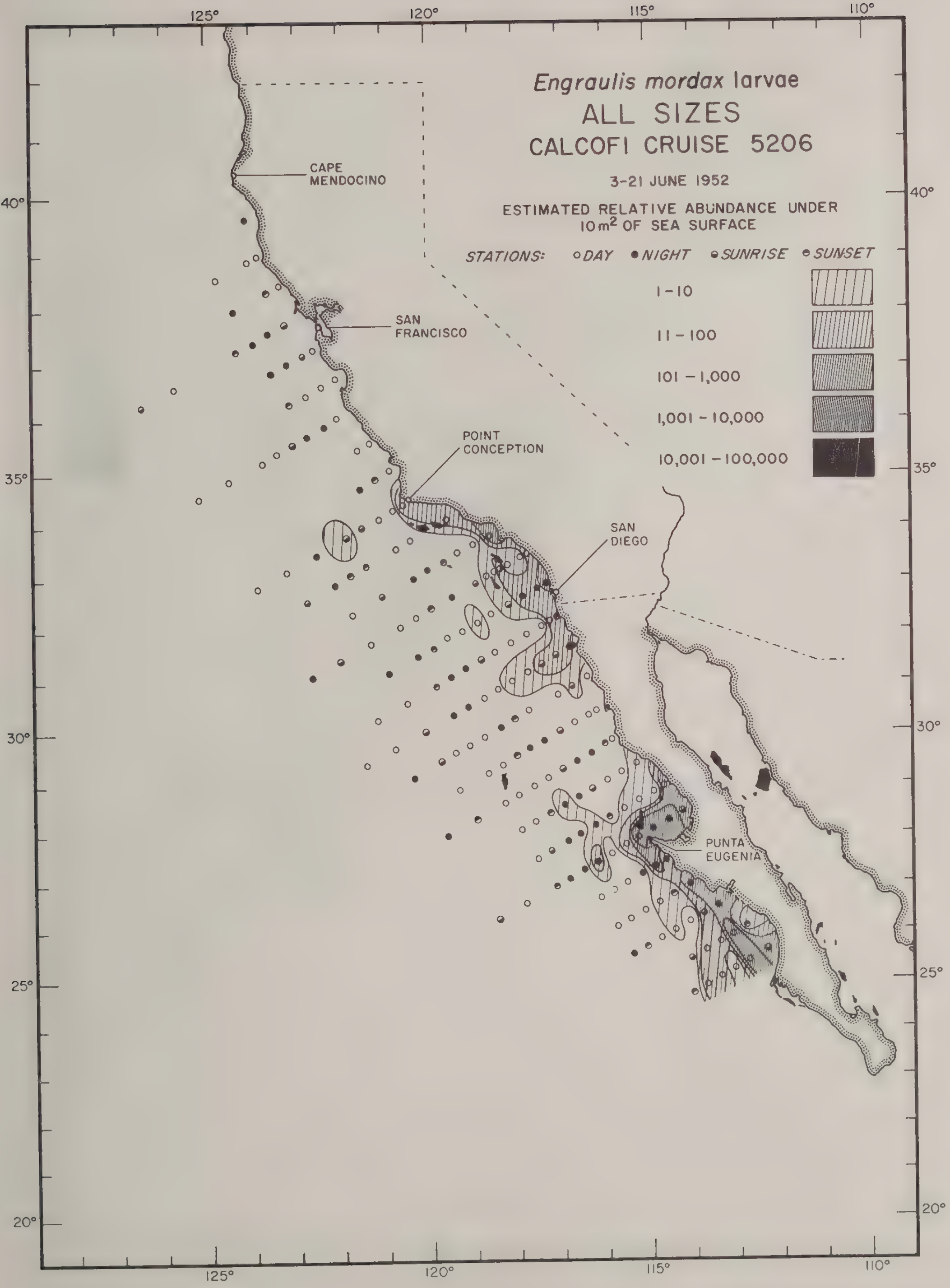
5205


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5206
3-21 JUNE 1952
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

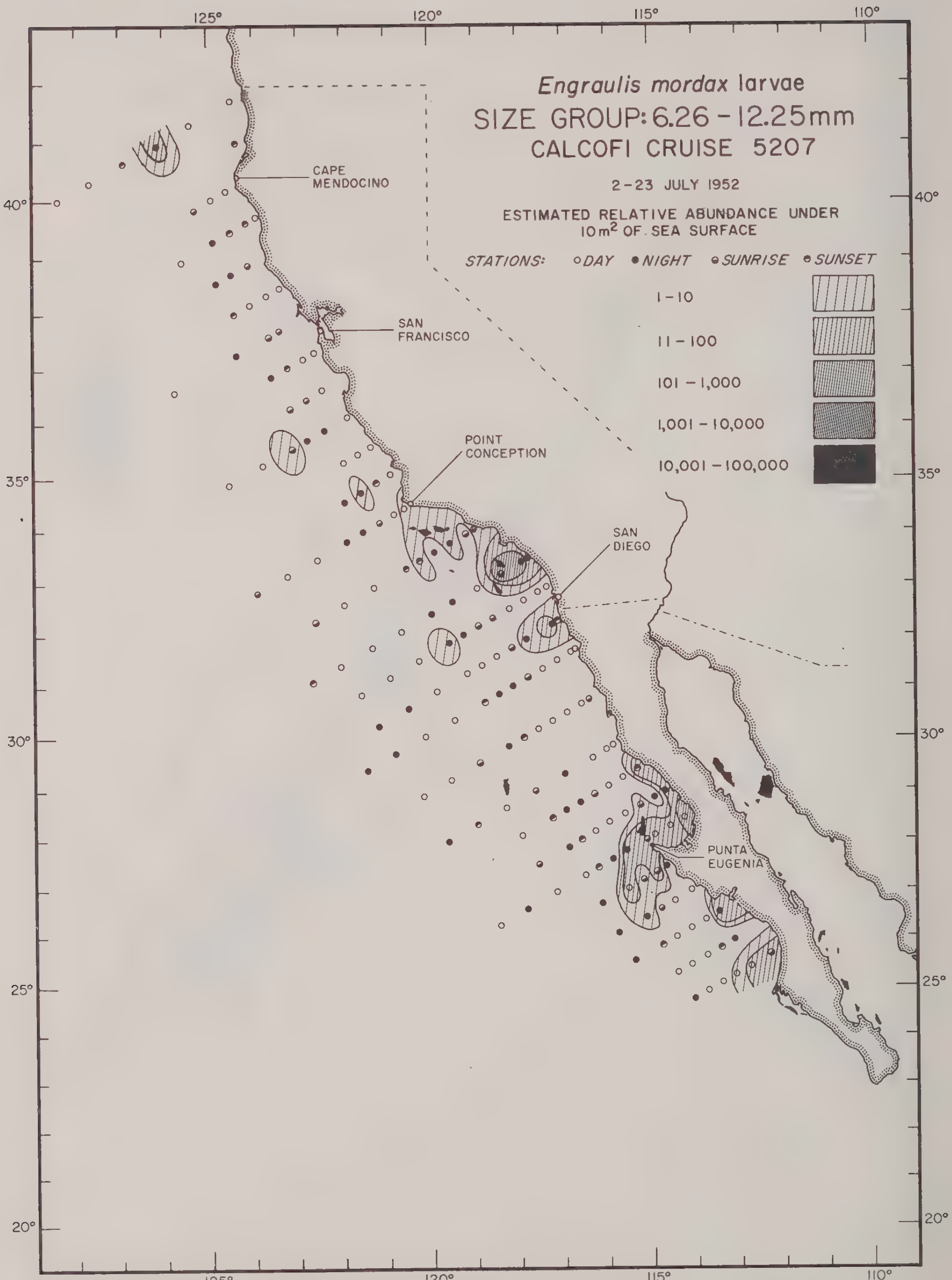
5206


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5206
3-21 JUNE 1952
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

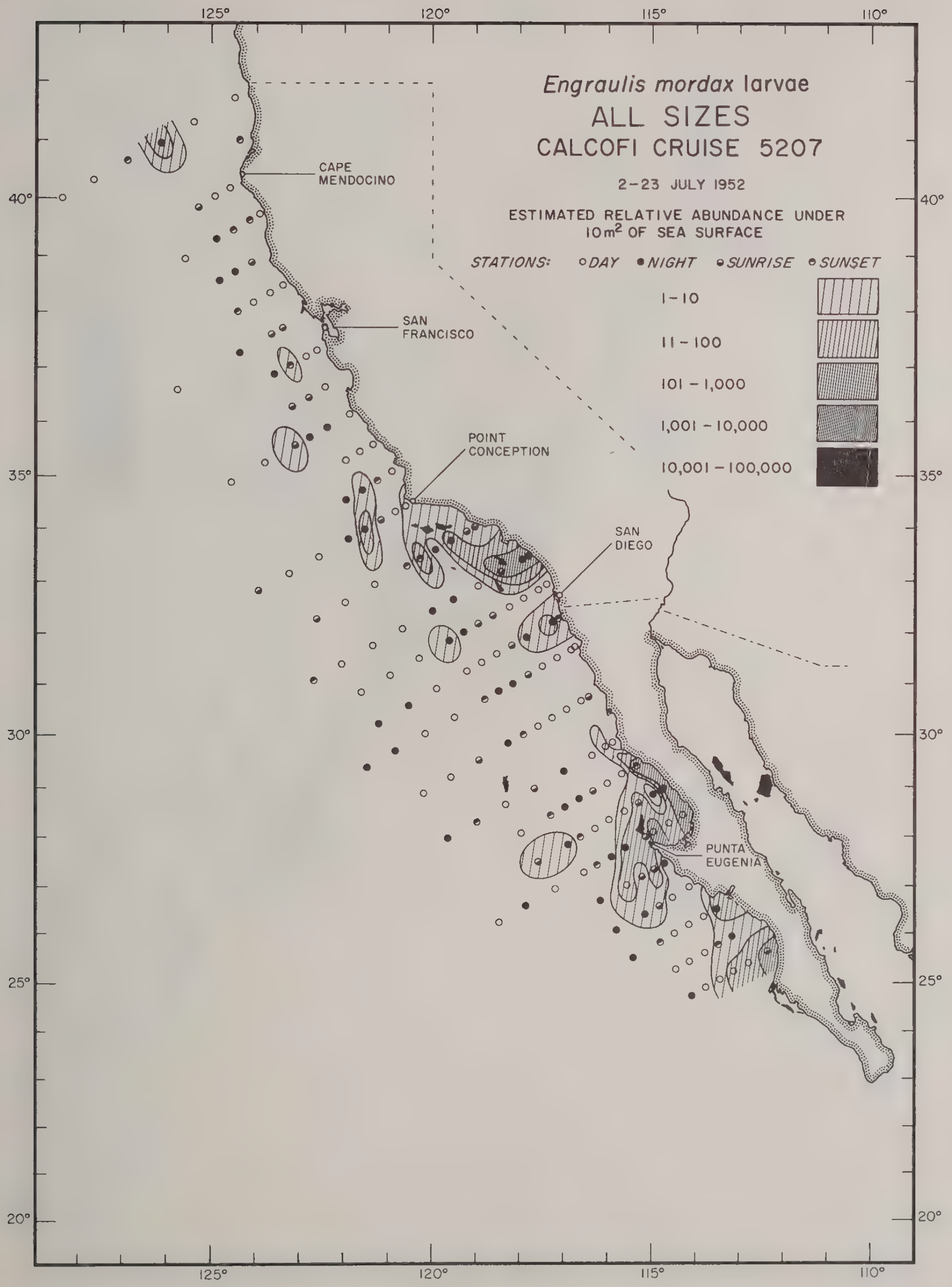
5206


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5207
2-23 JULY 1952
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

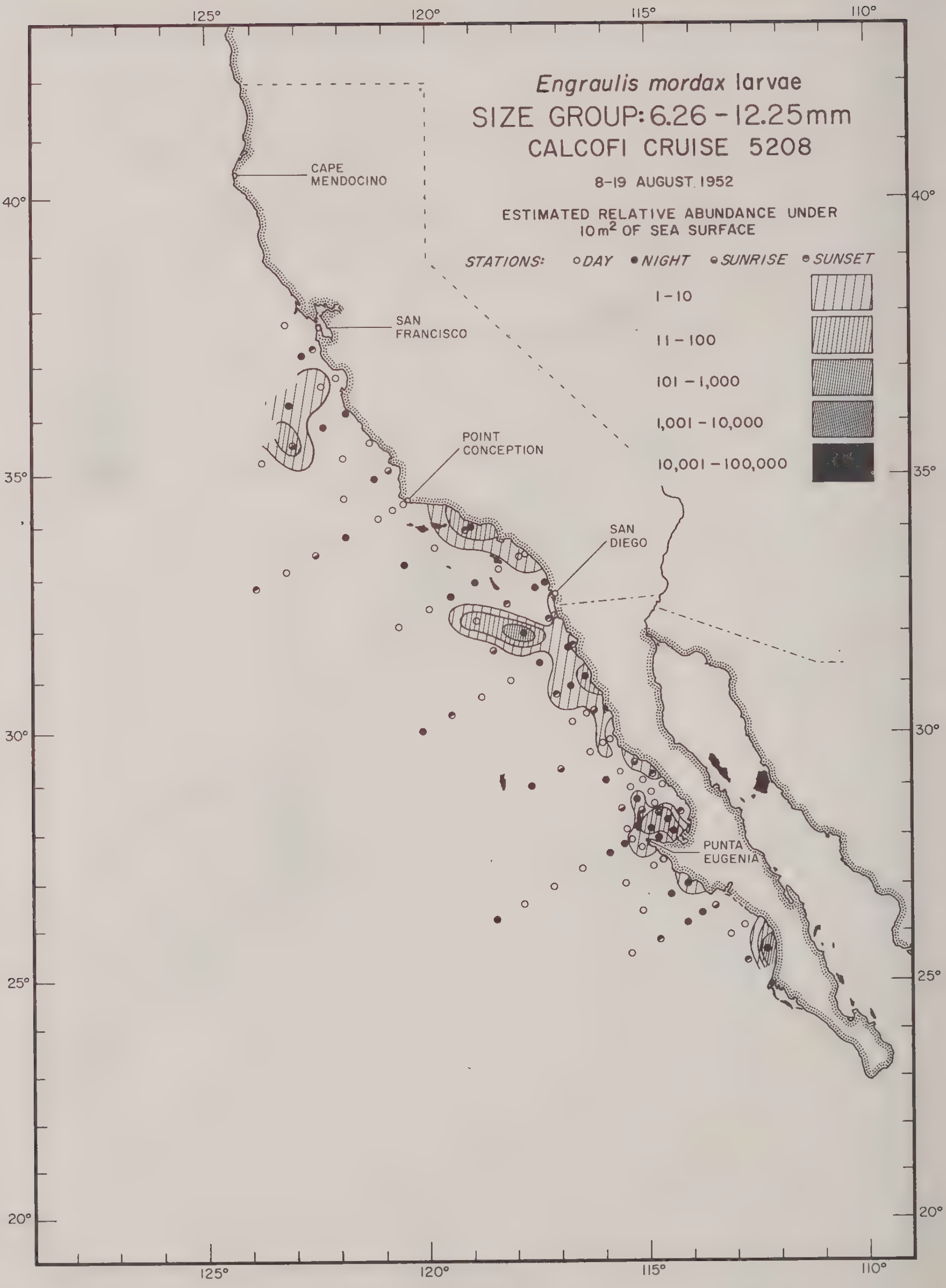
Size Group: 6.26-12.25mm

5207


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5207
2–23 JULY 1952
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1–10
11–100
101–1,000
1,001–10,000
10,001–100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

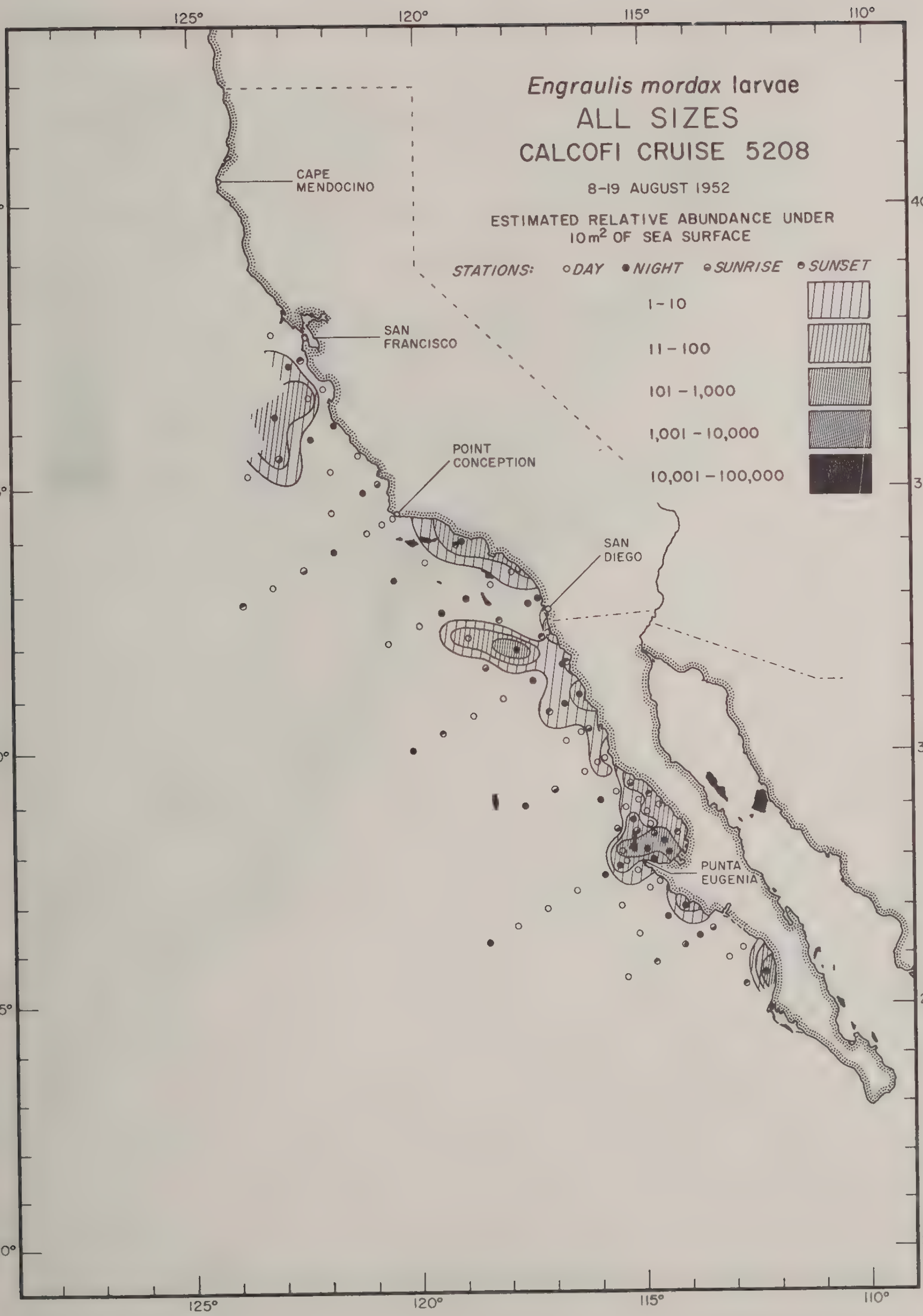
All Sizes
5207


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5208
8-19 AUGUST 1952
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◐ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

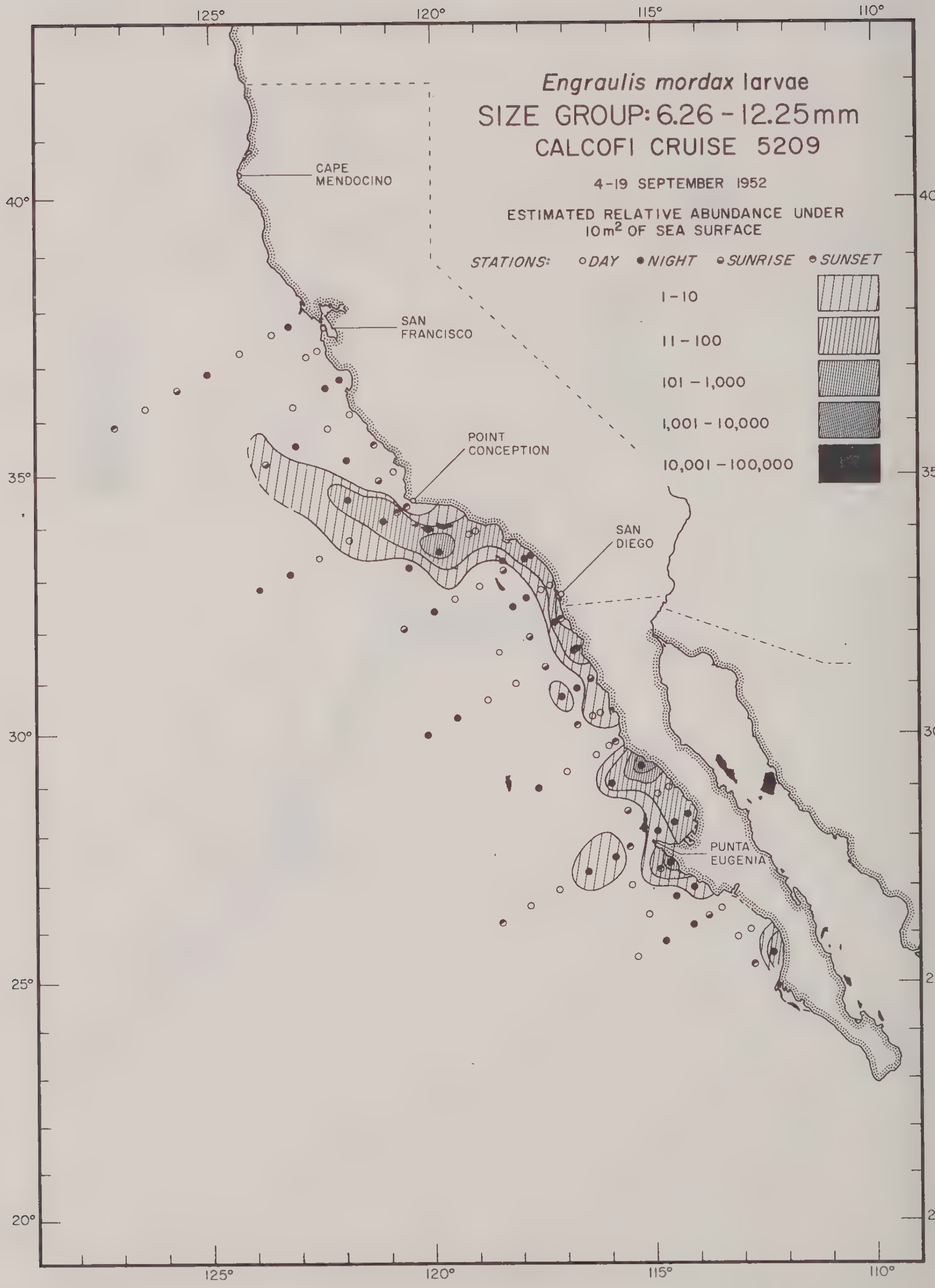
5208


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5208
8-19 AUGUST 1952
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◐SUNRISE ◑SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

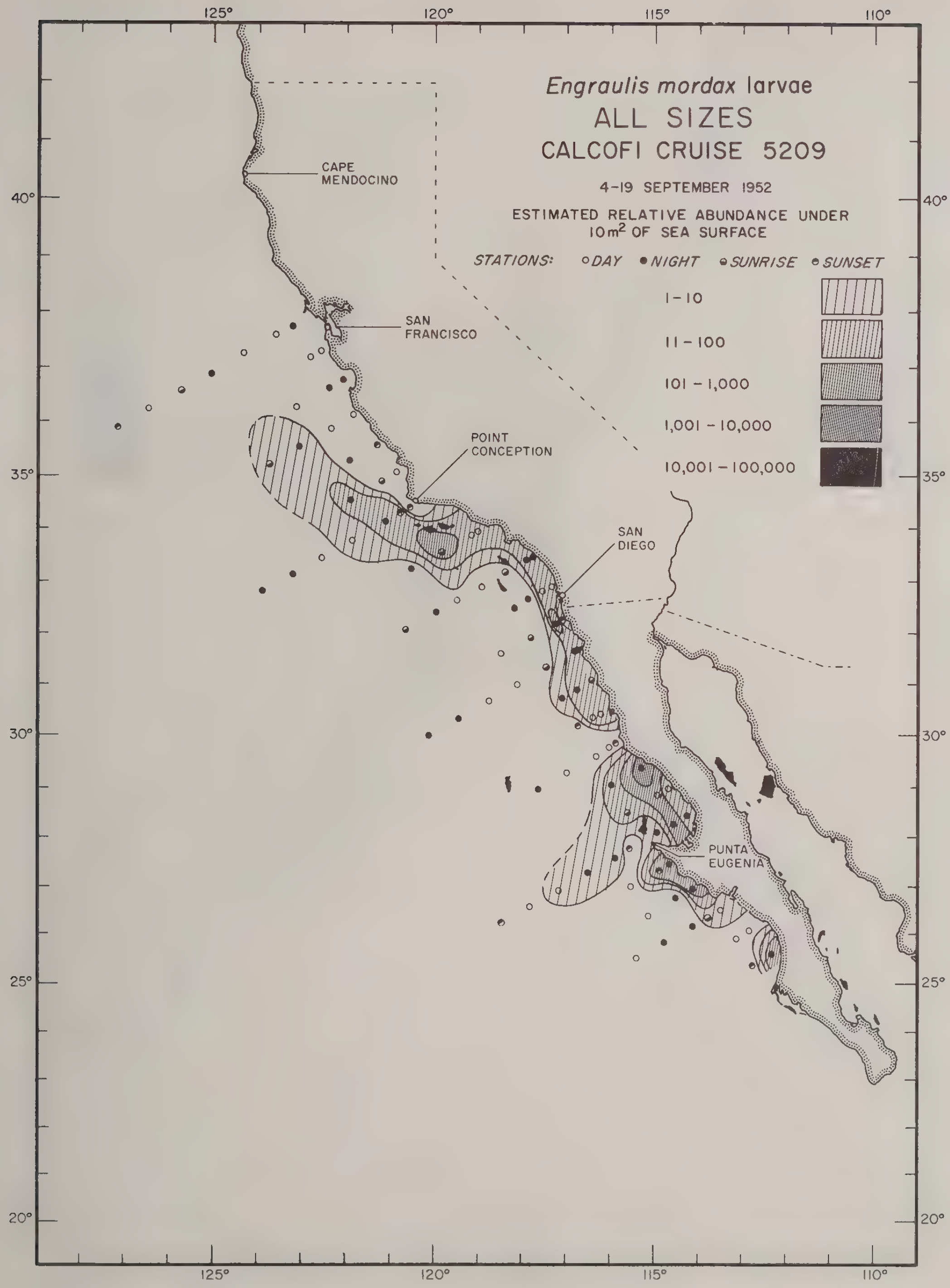
5208


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5209
4-19 SEPTEMBER 1952
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

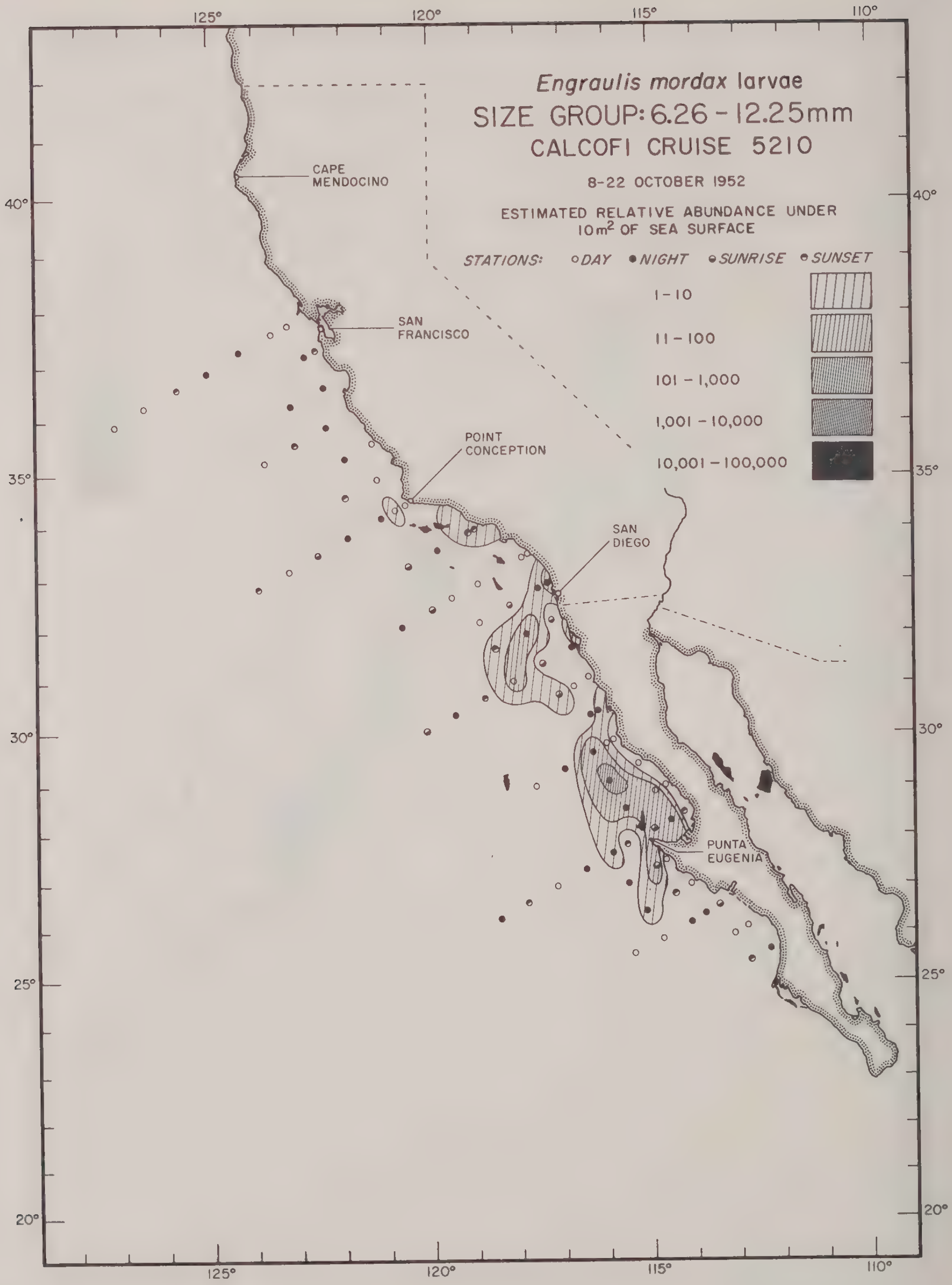
Size Group: 6.26-12.25mm

5209


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5209
4-19 SEPTEMBER 1952
ESTIMATED RELATIVE ABUNDANCE UNDER
$10 m^2$ OF SEA SURFACE
STATIONS: ○ *DAY* ● *NIGHT* ◒ *SUNRISE* ◓ *SUNSET*
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

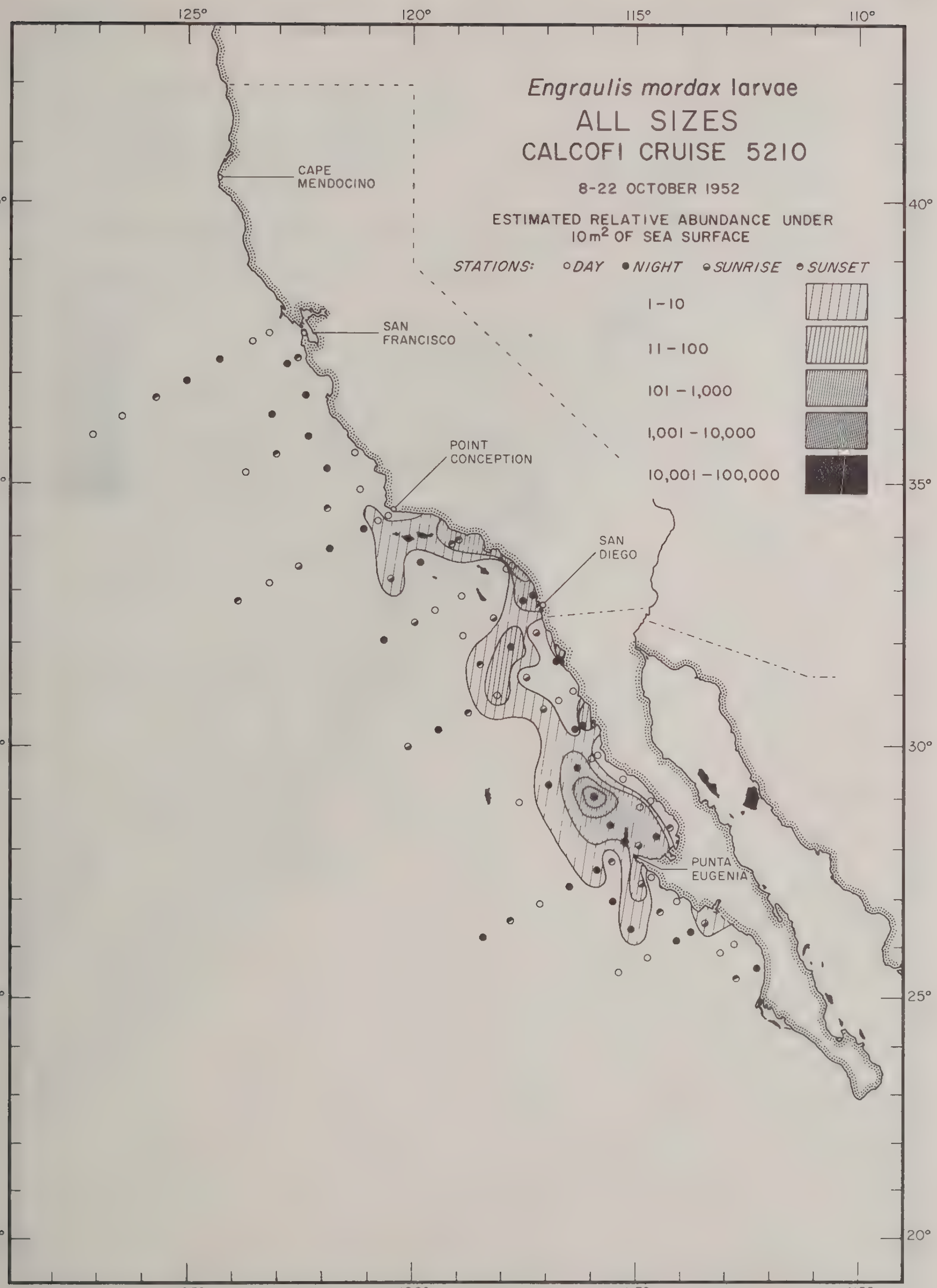
All Sizes
5209


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5210
8-22 OCTOBER 1952
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ *DAY* ● *NIGHT* *SUNRISE* *SUNSET*
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

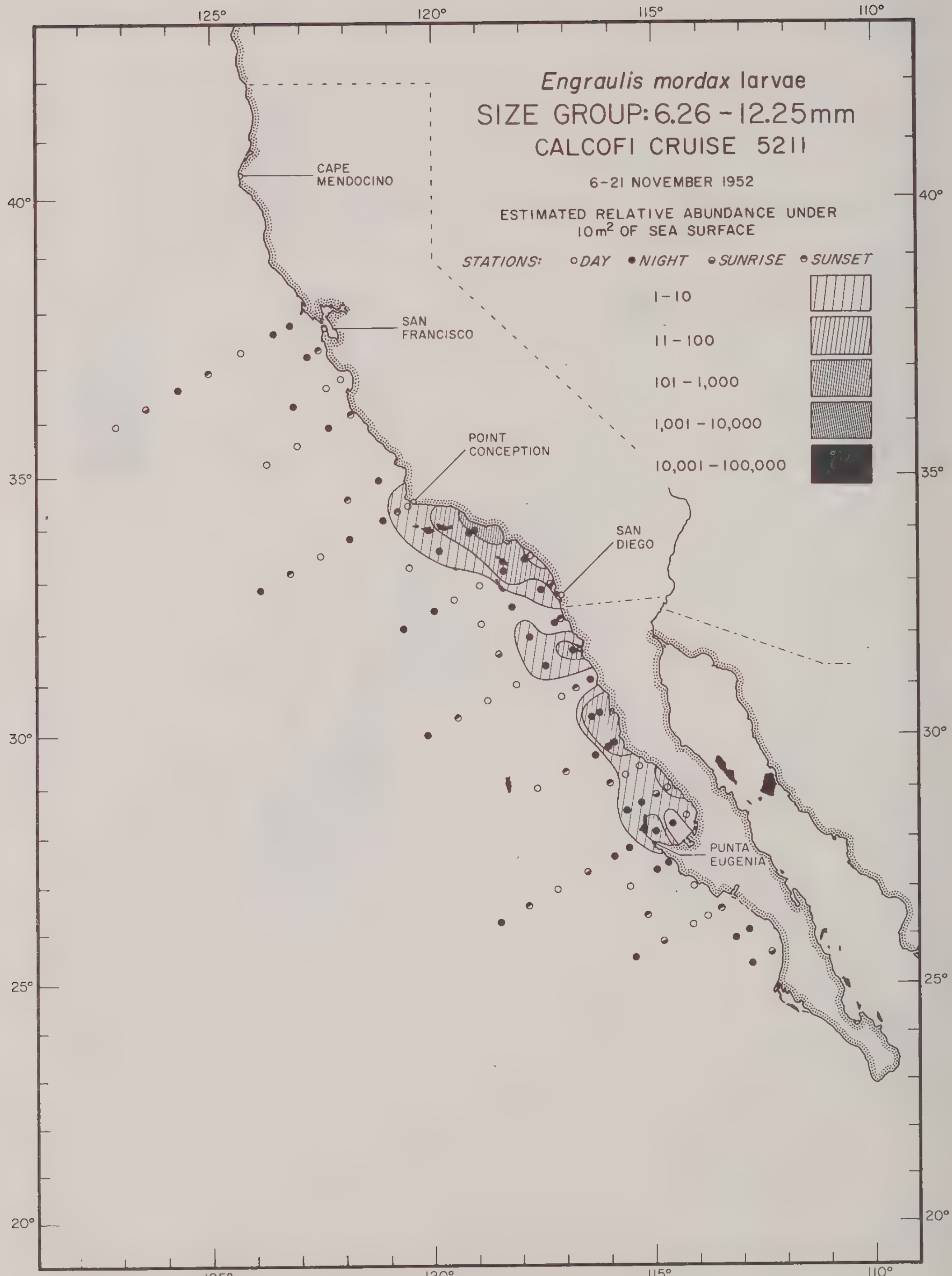
5210


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5210
8-22 OCTOBER 1952
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

All Sizes

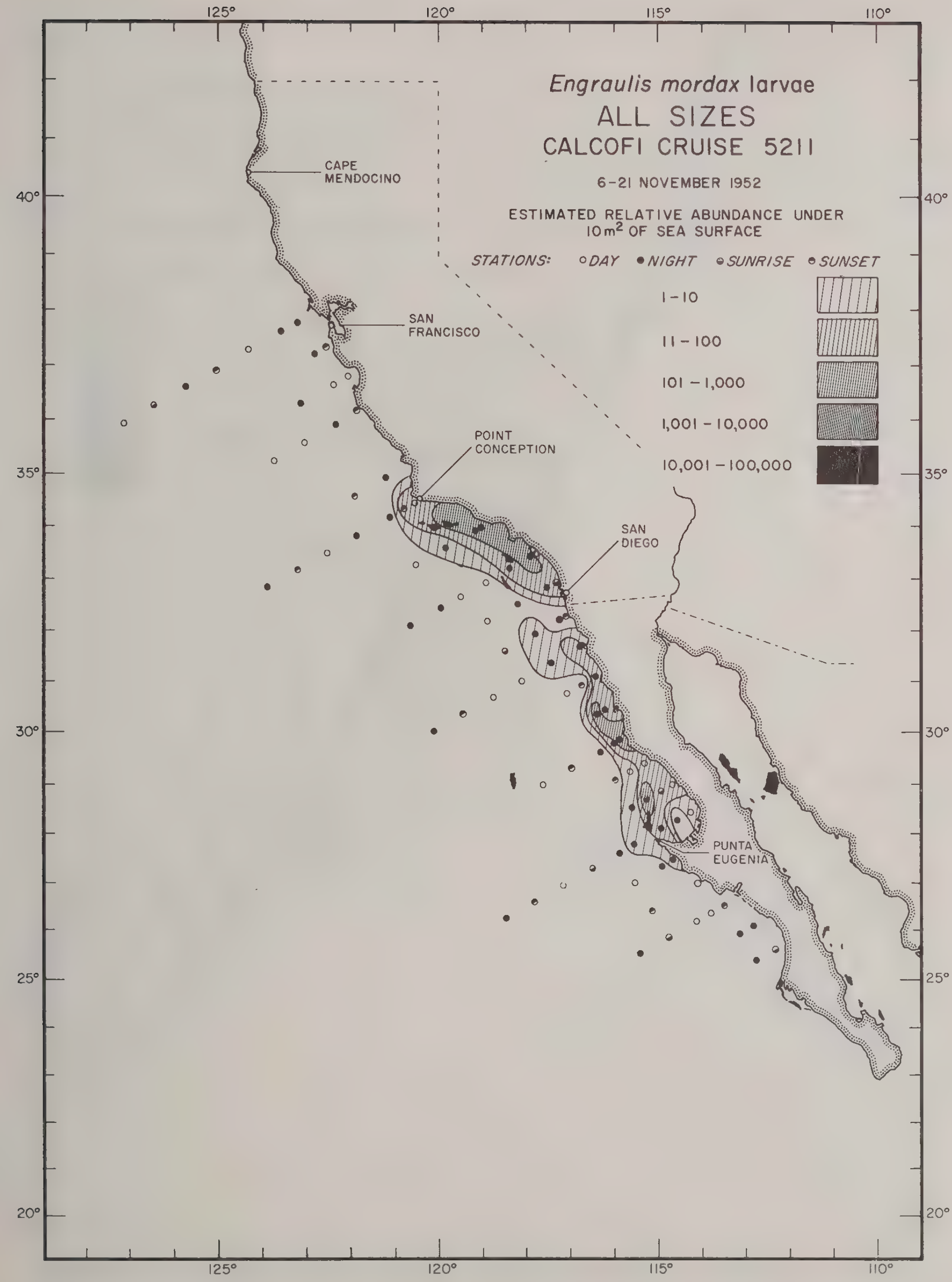
5210


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5211
6-21 NOVEMBER 1952
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

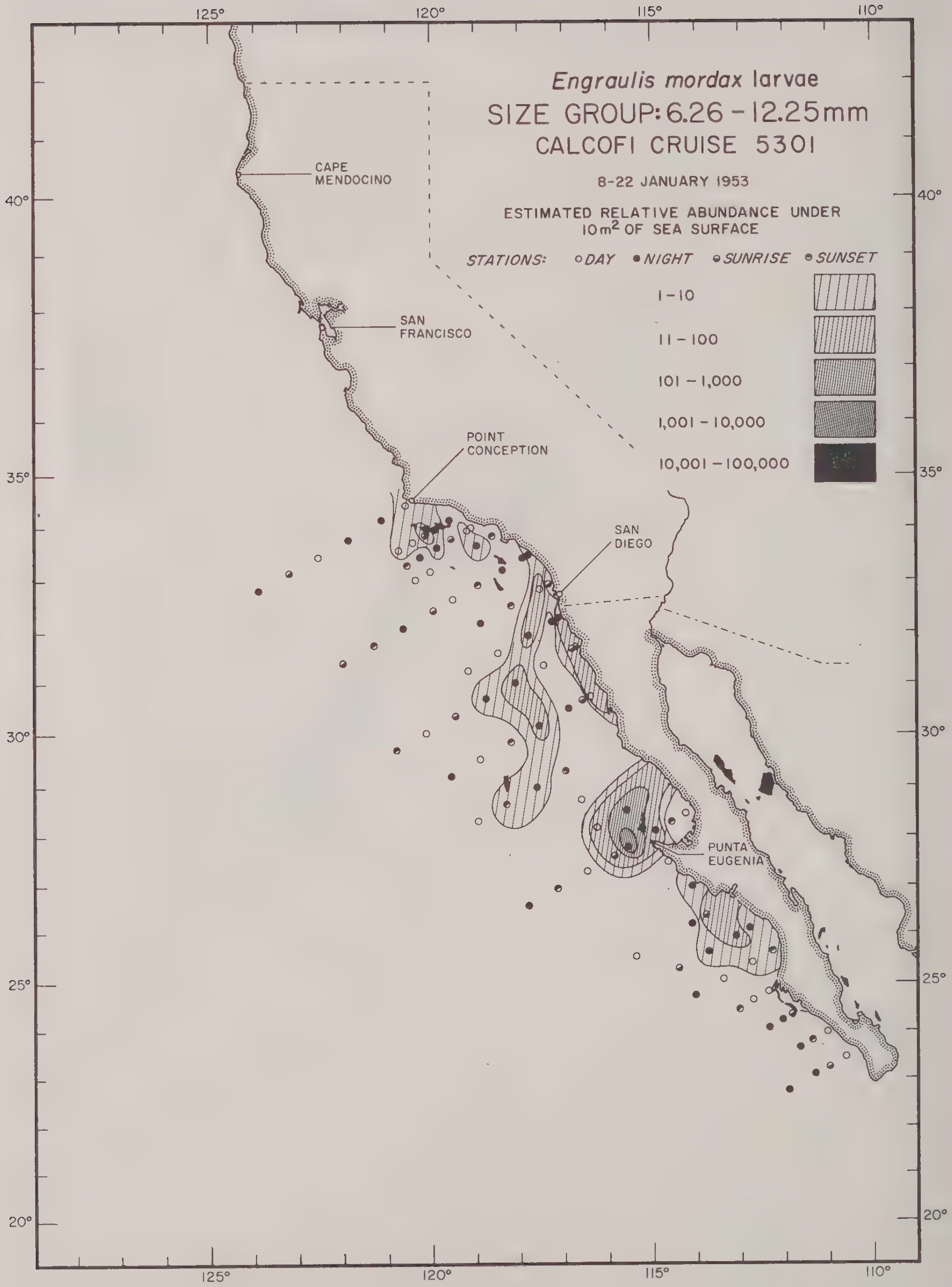
5211


125°
120°
115°
110°
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5211
6-21 NOVEMBER 1952
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

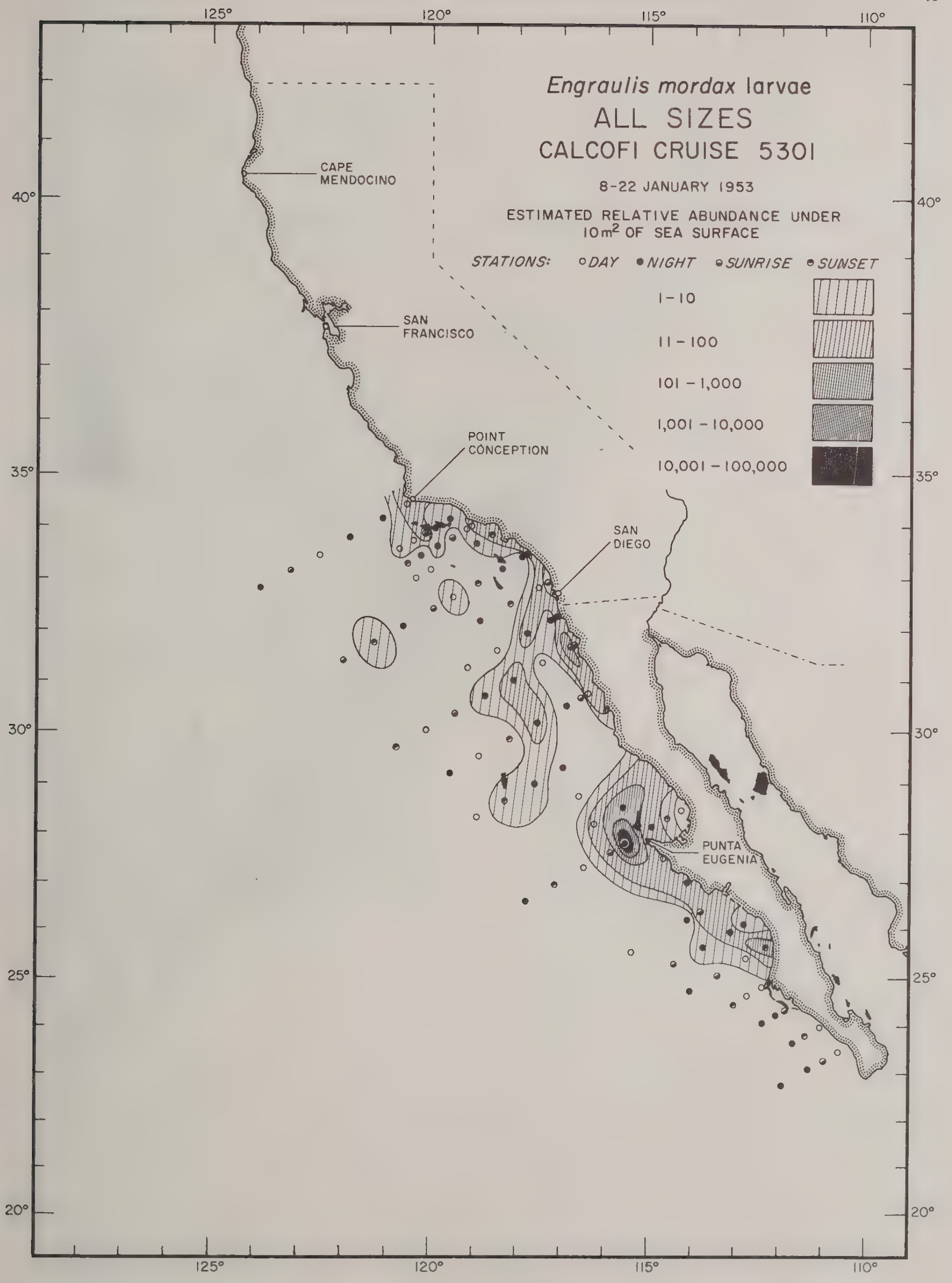
5211


125°
120°
115°
110°
Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5301
8-22 JANUARY 1953
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

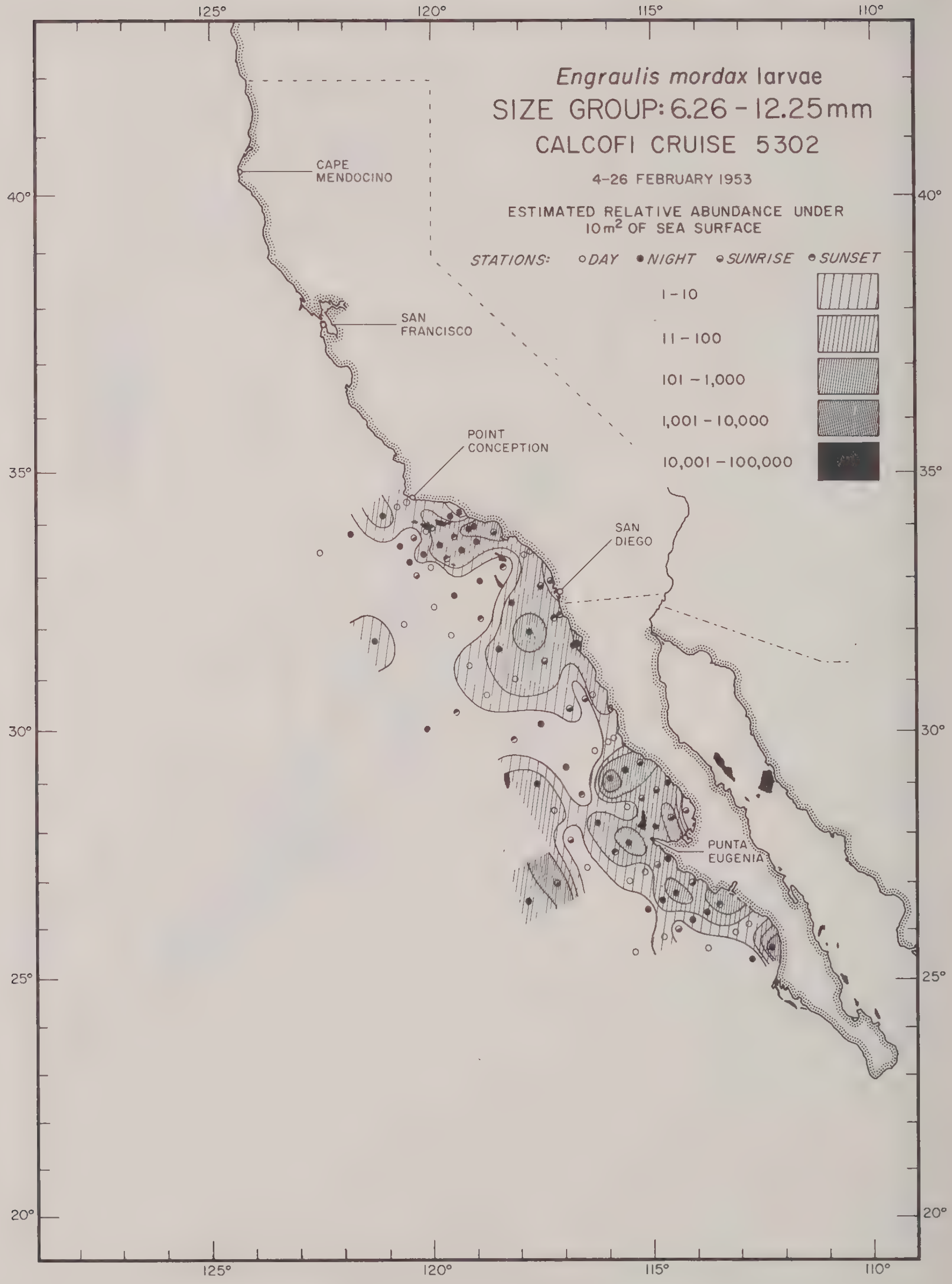
5301


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5301
8-22 JANUARY 1953
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

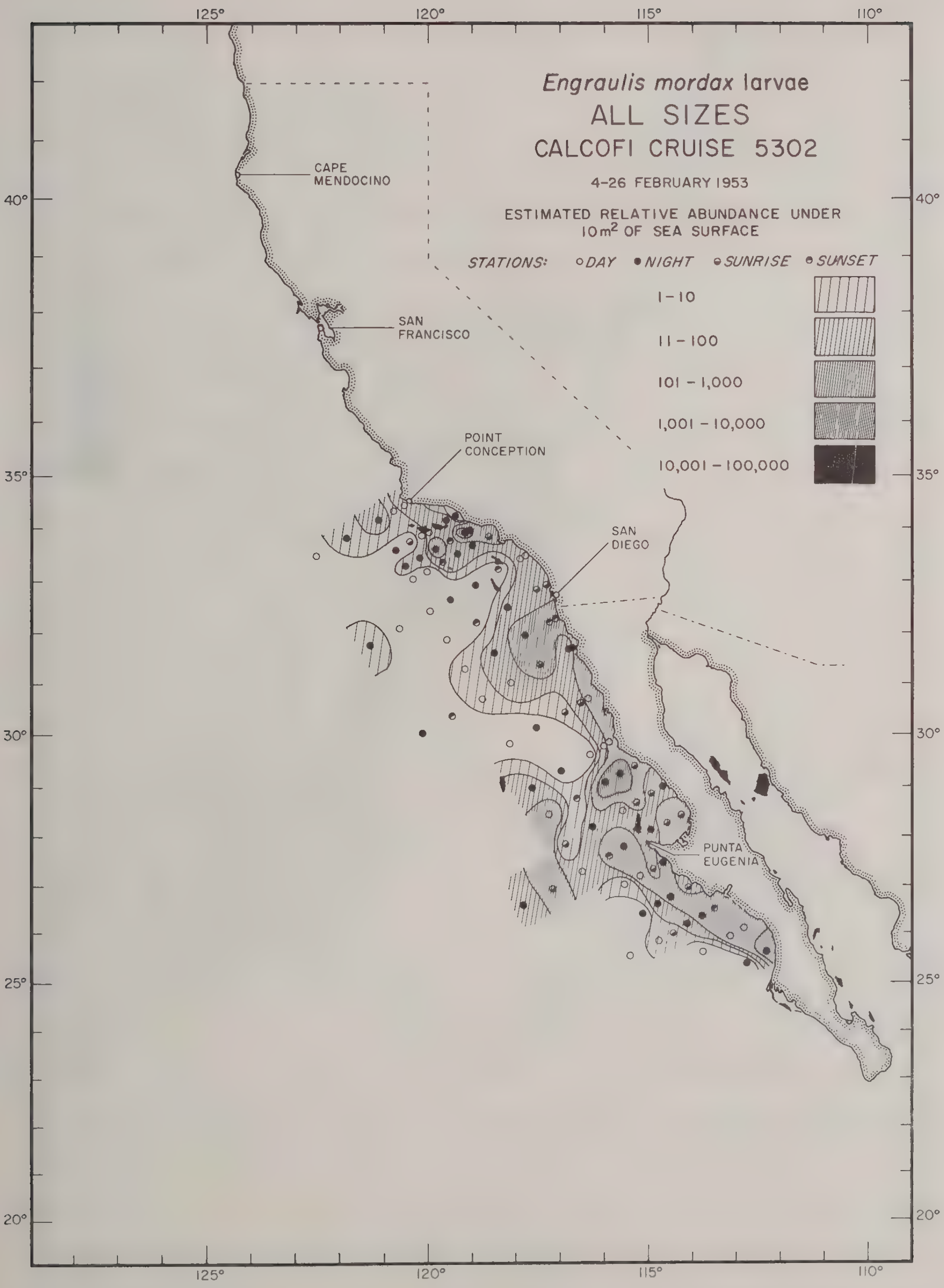
5301


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5302
4-26 FEBRUARY 1953
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

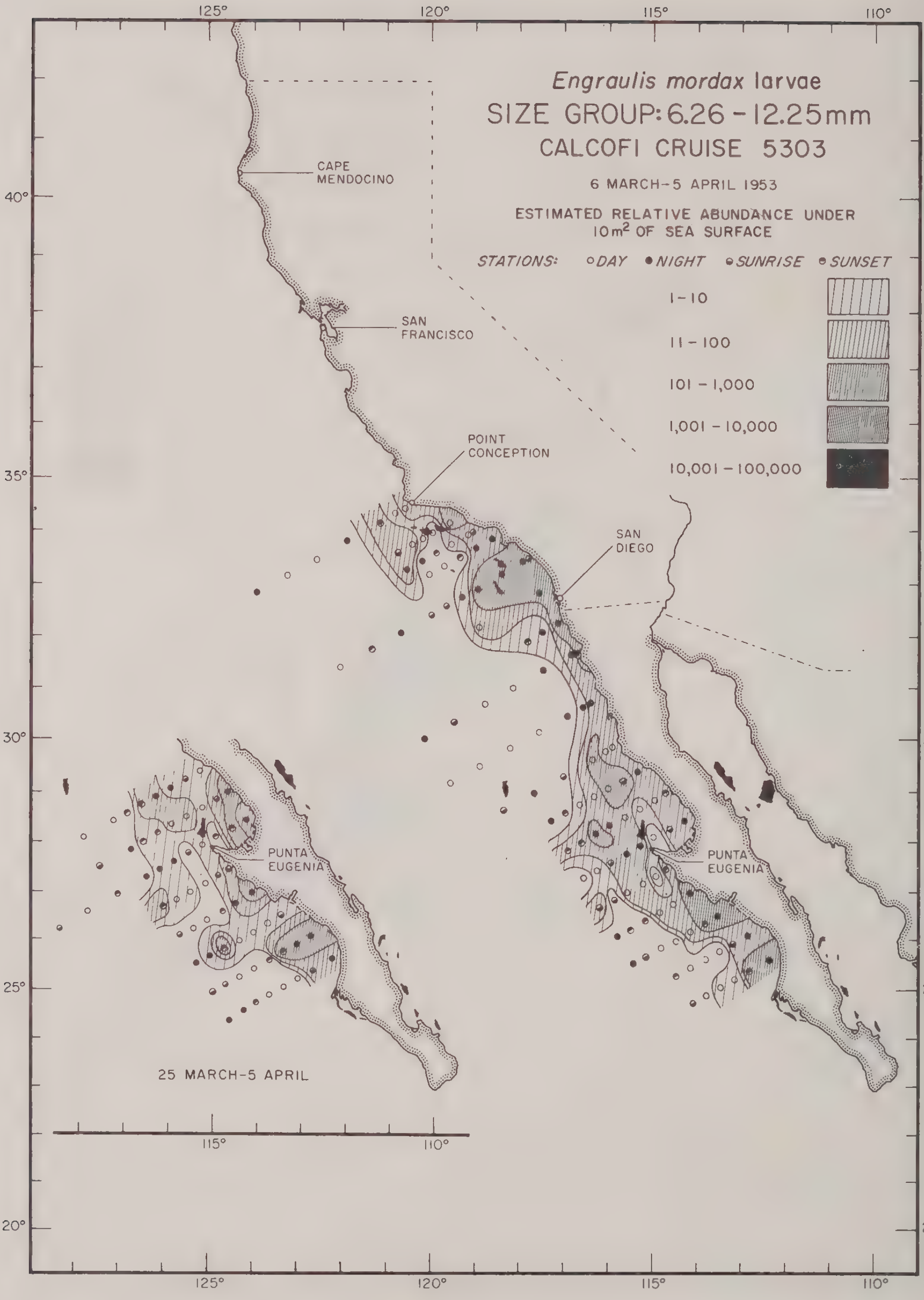
5302


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5302
4-26 FEBRUARY 1953
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT SUNRISE SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

All Sizes

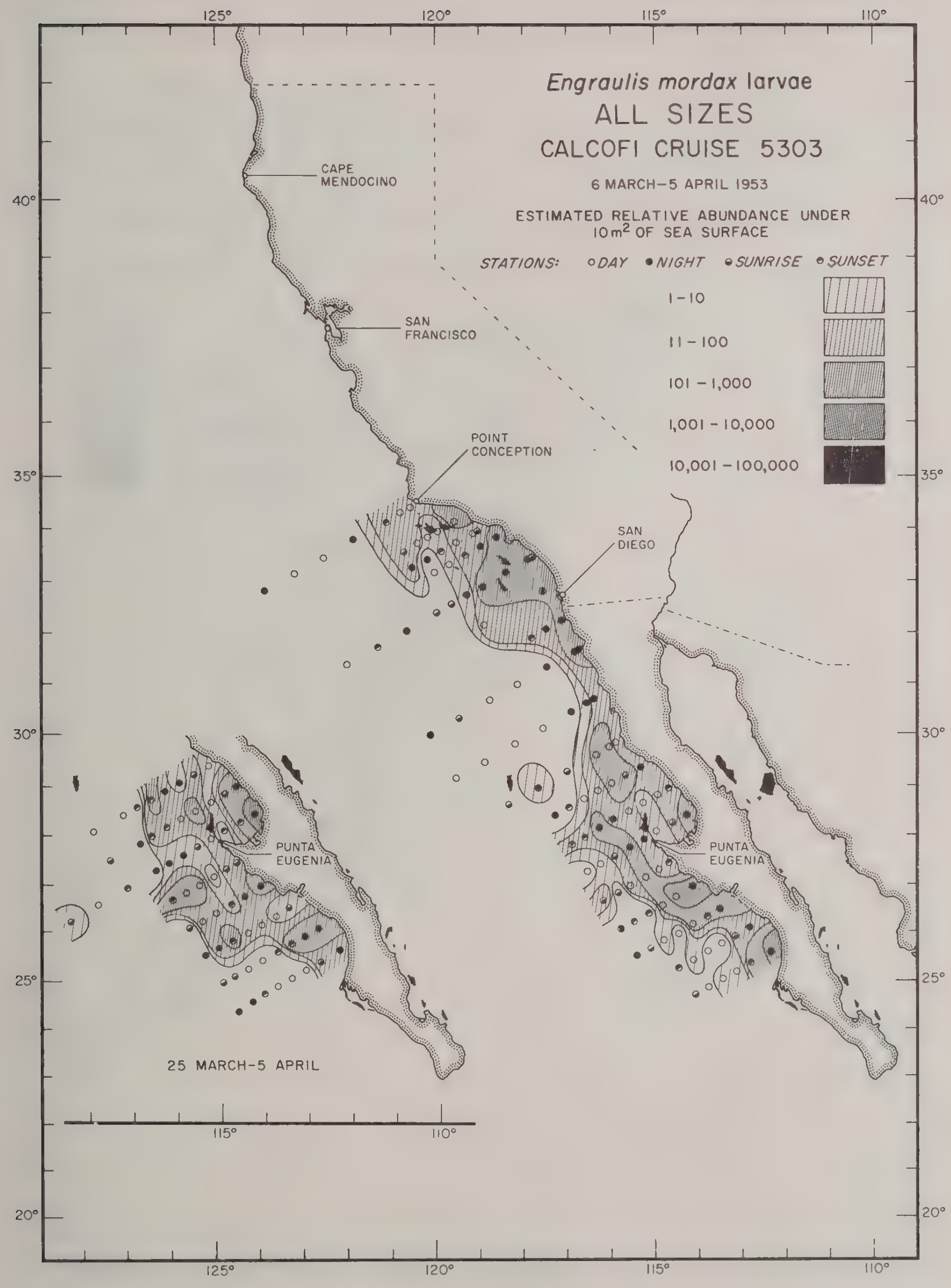
5302


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5303
6 MARCH-5 APRIL 1953
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT SUNRISE SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
PUNTA EUGENIA
25 MARCH-5 APRIL
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

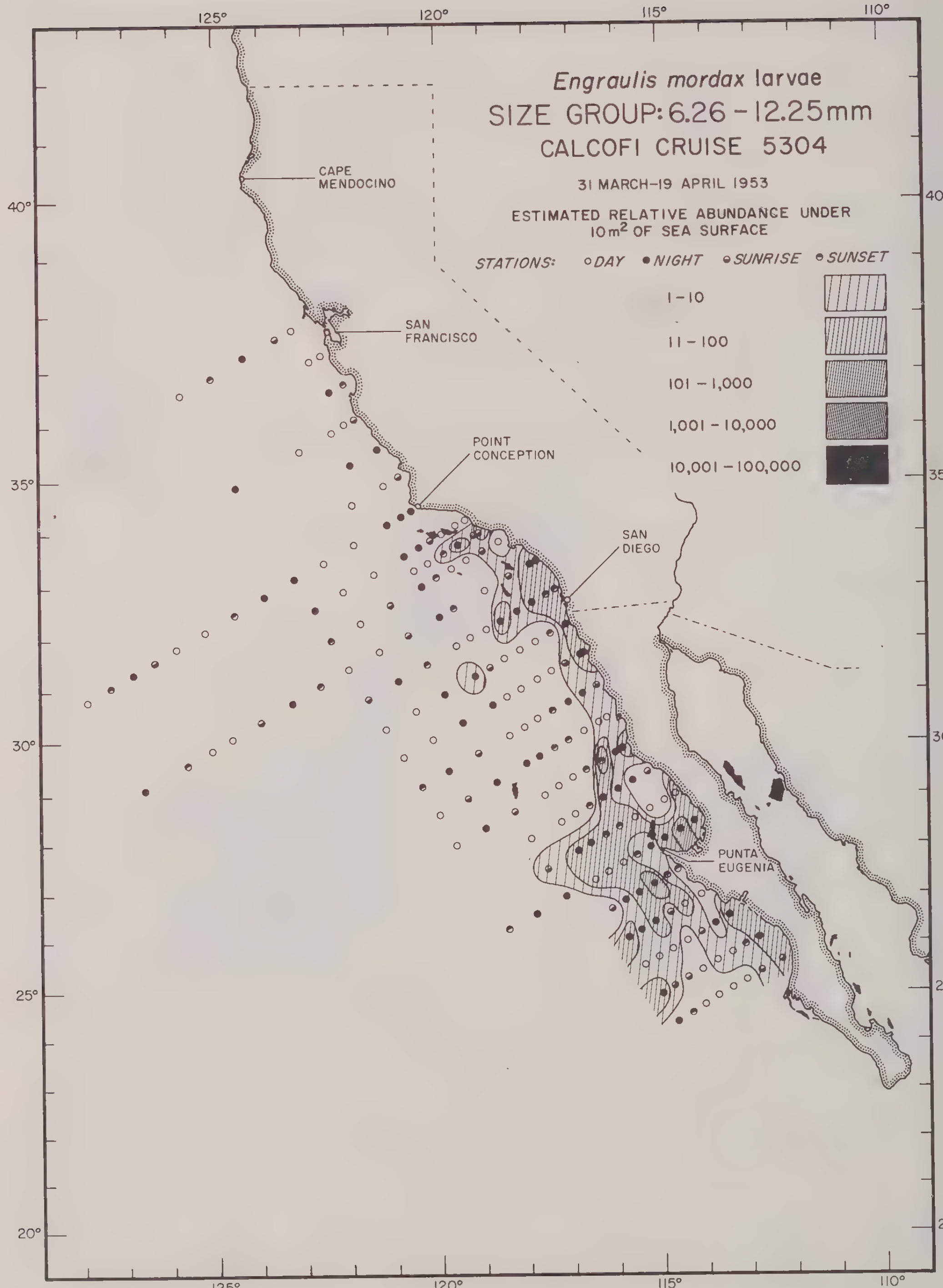
5303


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5303
6 MARCH–5 APRIL 1953
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
PUNTA EUGENIA
25 MARCH–5 APRIL
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

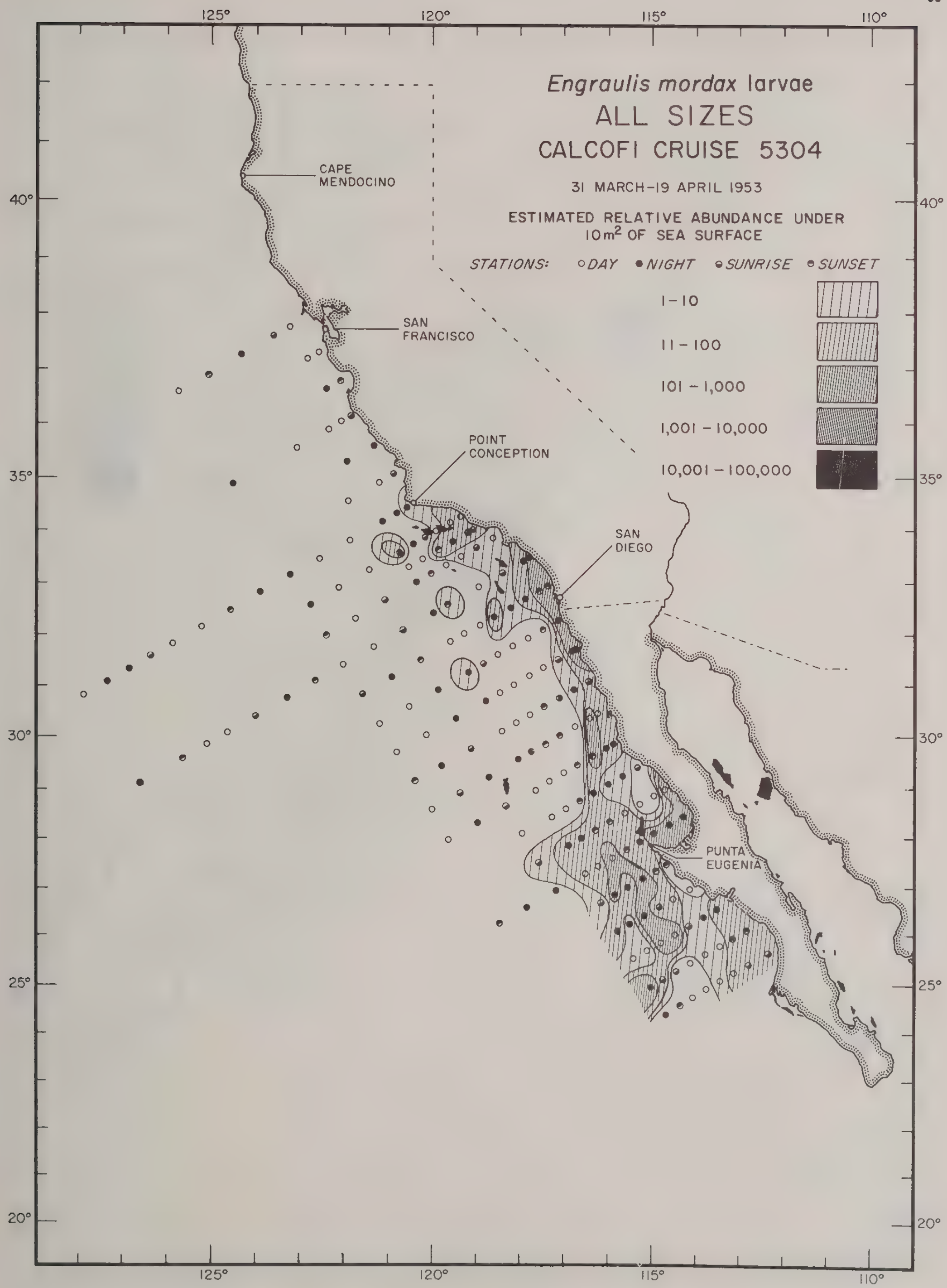
5303


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5304
31 MARCH-19 APRIL 1953
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

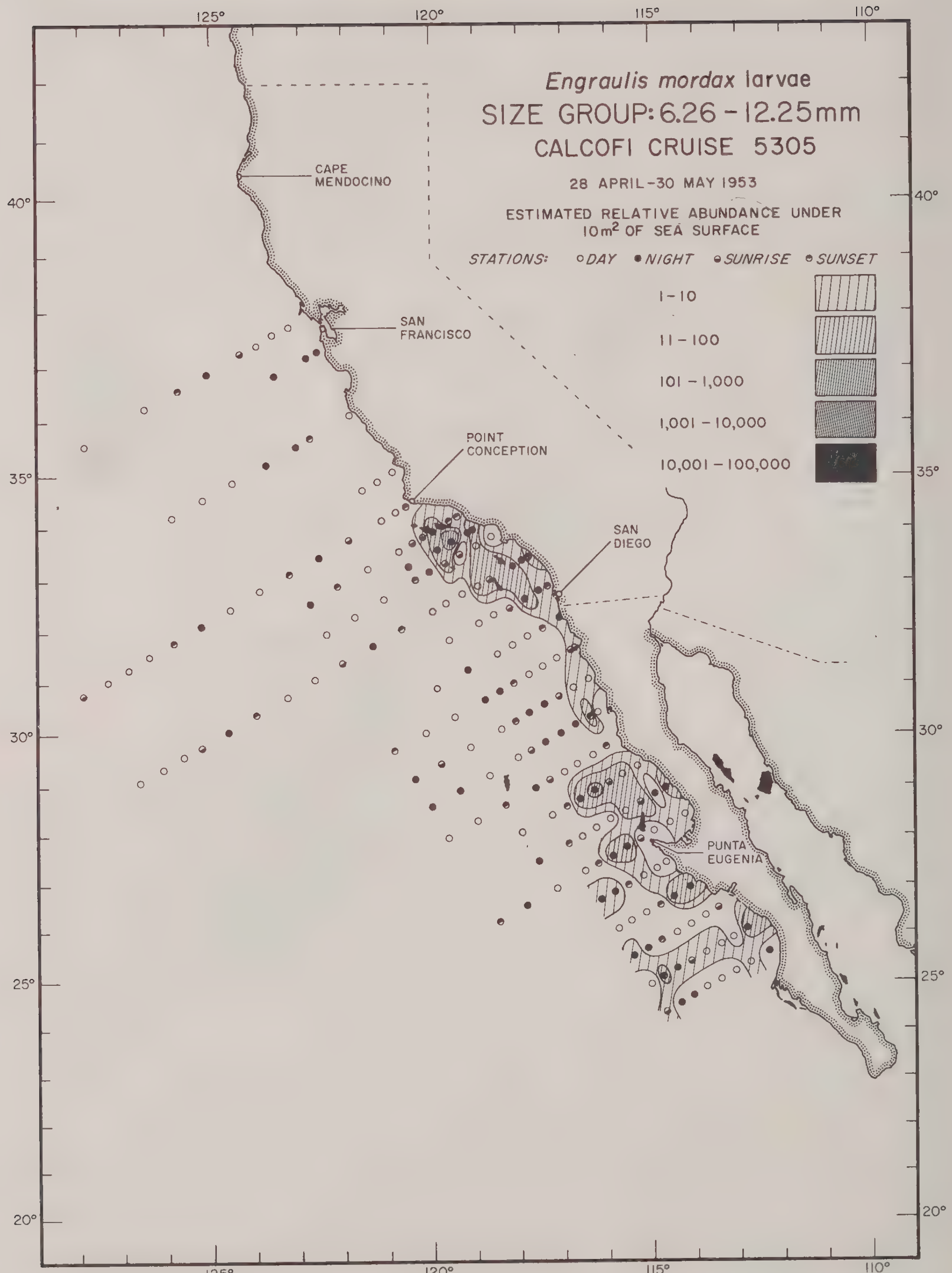
5304


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5304
31 MARCH–19 APRIL 1953
ESTIMATED RELATIVE ABUNDANCE UNDER
$10 m^2$ OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1–10
11–100
101–1,000
1,001–10,000
10,001–100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

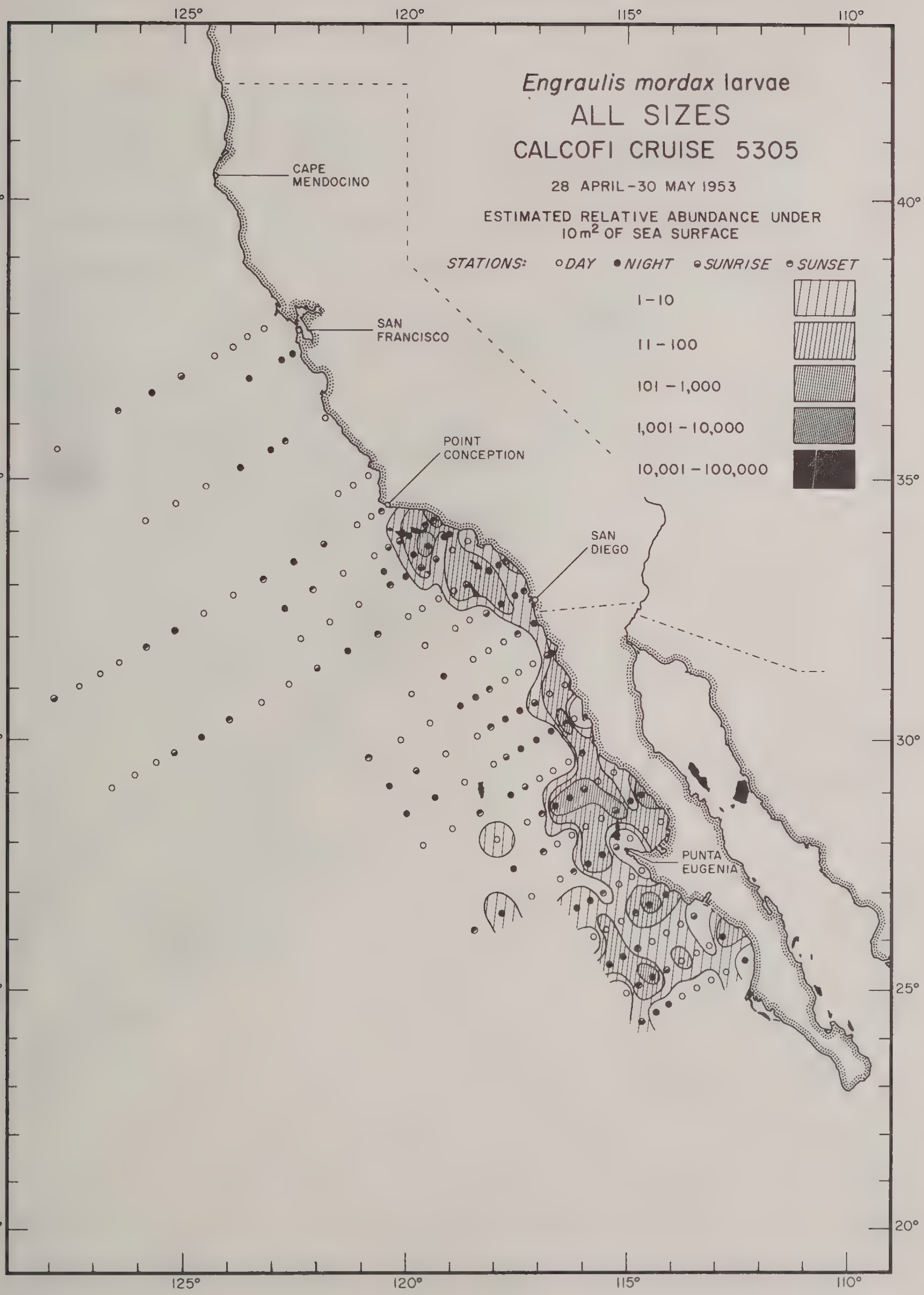
5304


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5305
28 APRIL - 30 MAY 1953
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

5305

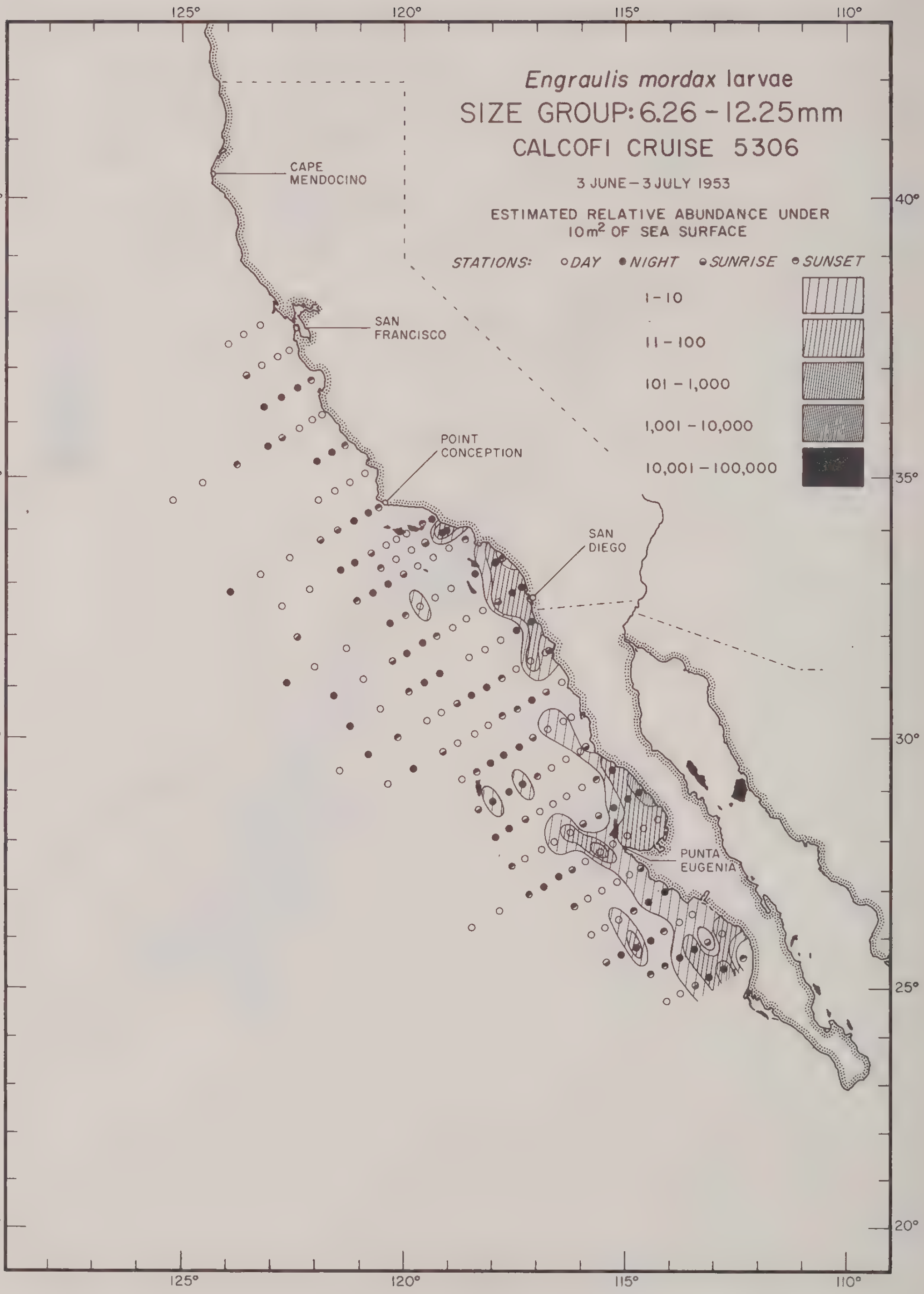


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5305
28 APRIL-30 MAY 1953
ESTIMATED RELATIVE ABUNDANCE UNDER
$10 m^2$ OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◐ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

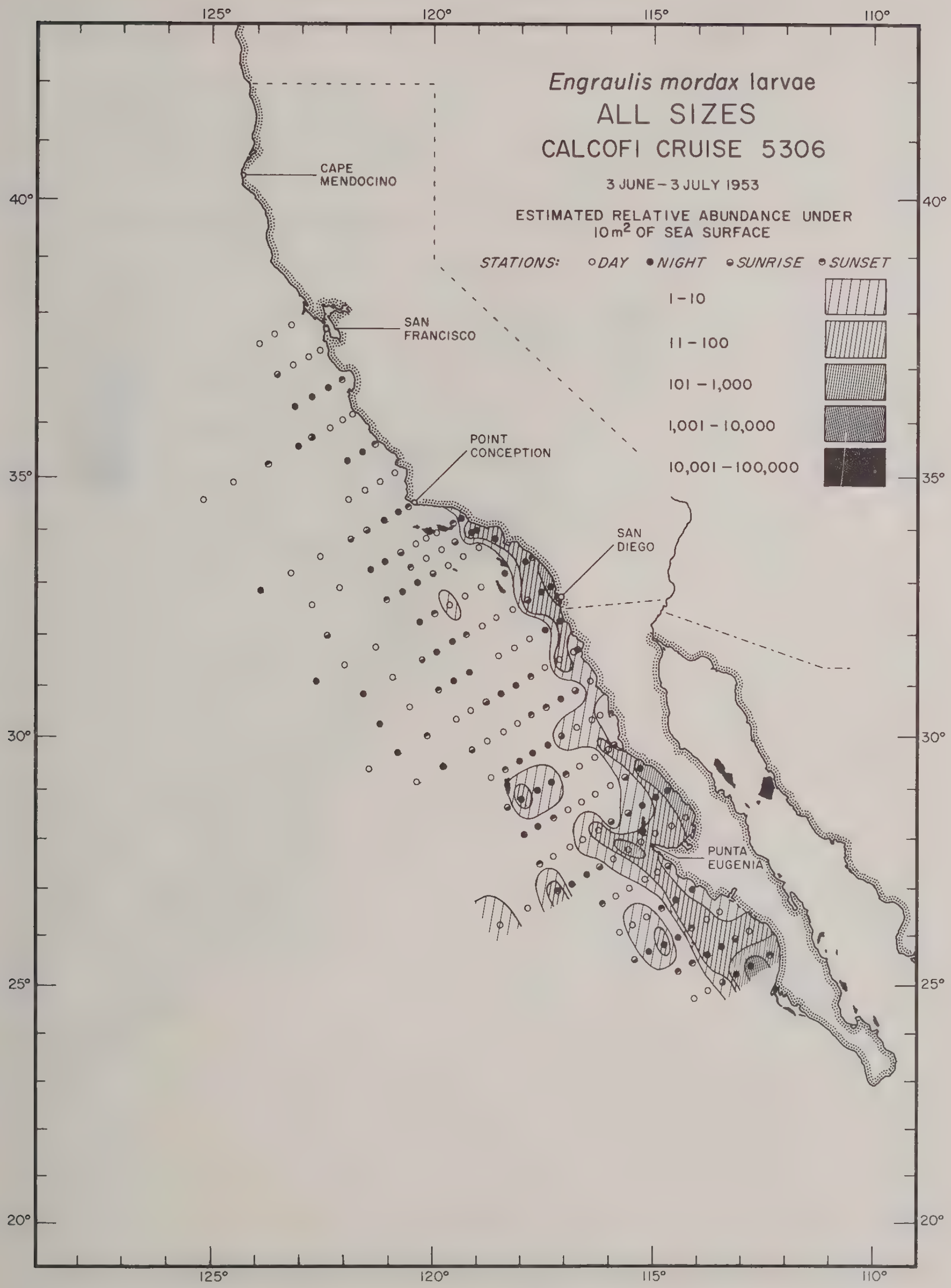
5305


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5306
3 JUNE - 3 JULY 1953
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

Size Group: 6.26-12.25mm

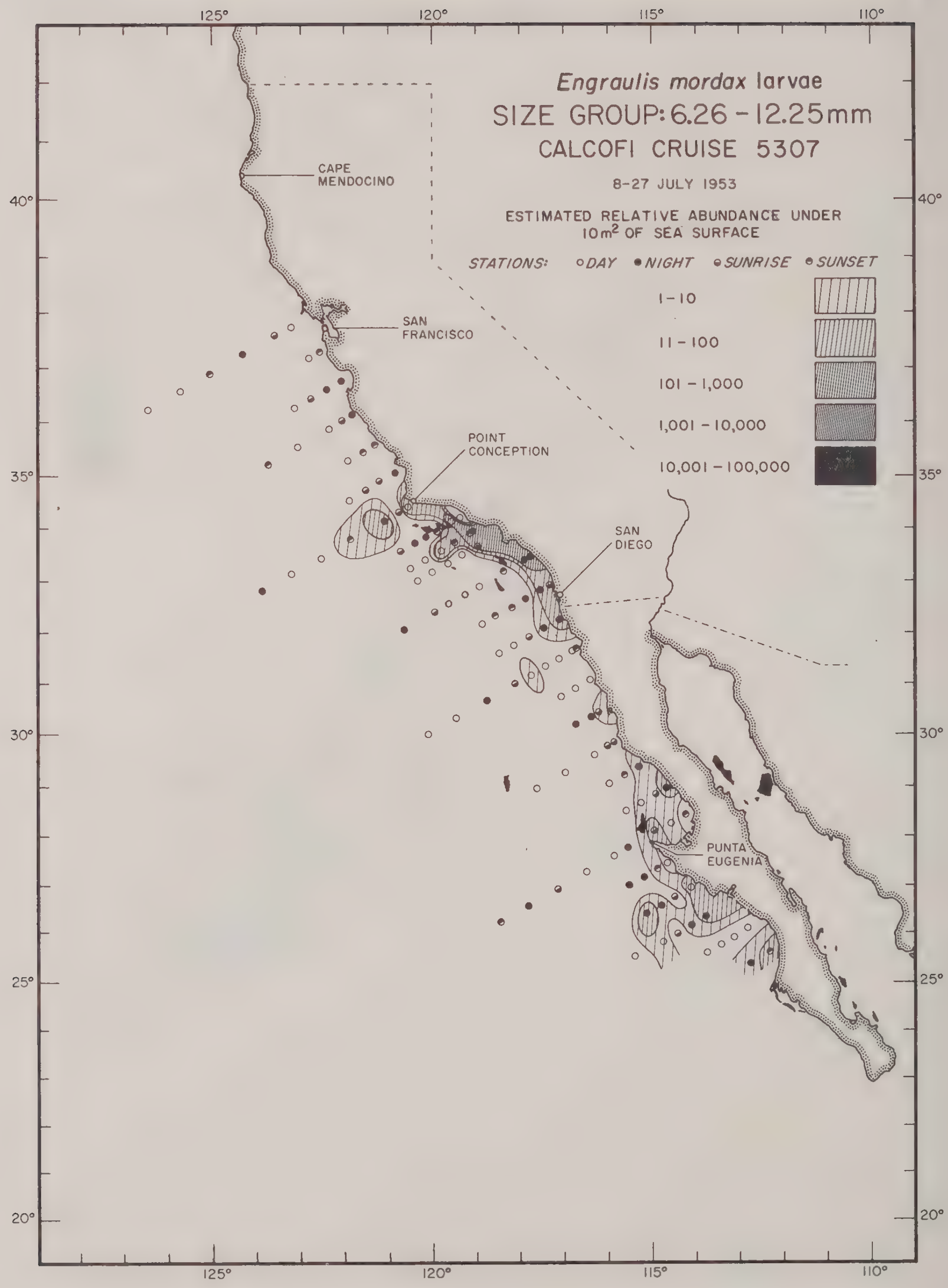
5306


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5306
3 JUNE – 3 JULY 1953
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

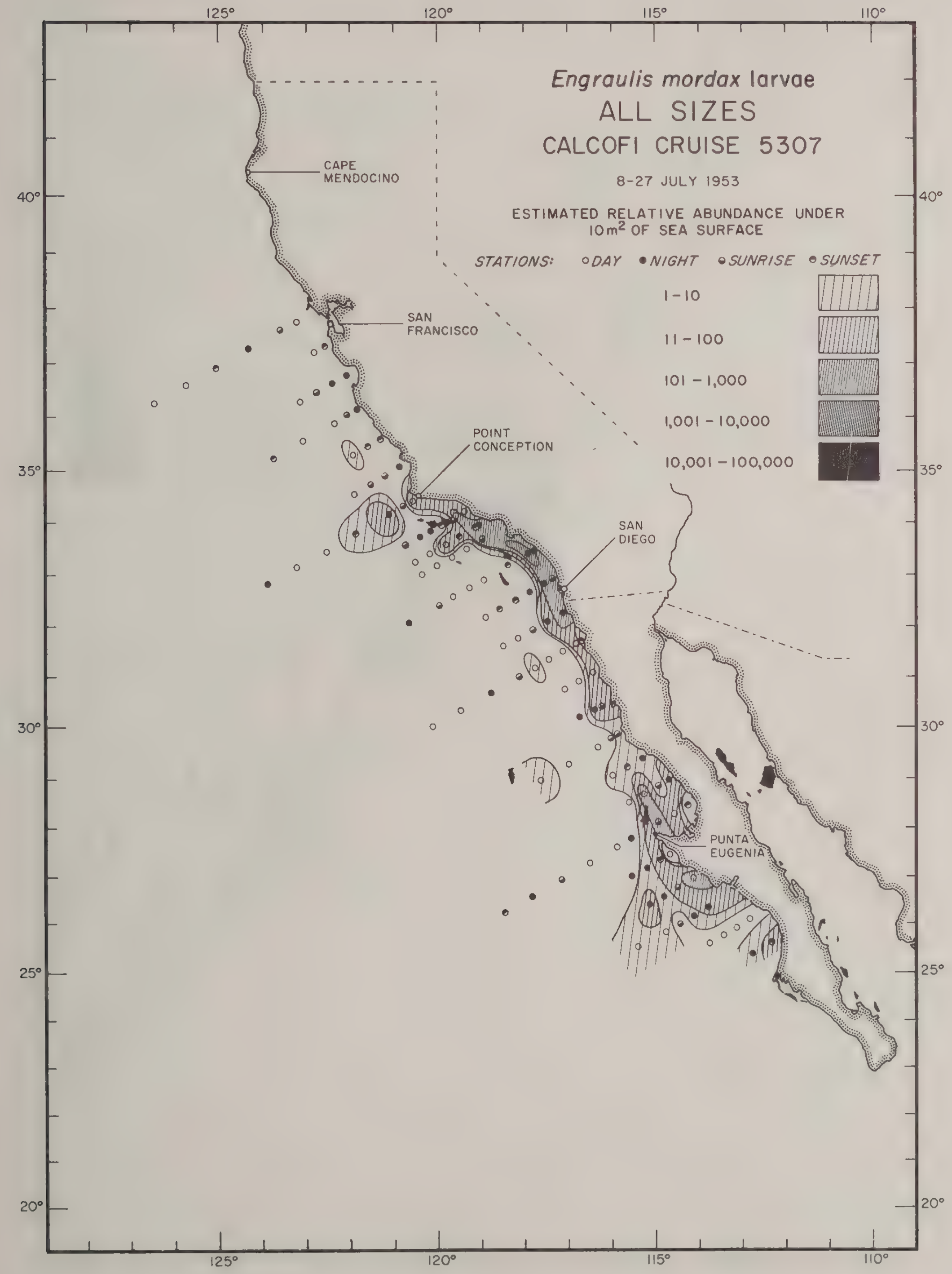
5306


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5307
8-27 JULY 1953
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ *DAY* ● *NIGHT* ◒ *SUNRISE* ◓ *SUNSET*
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

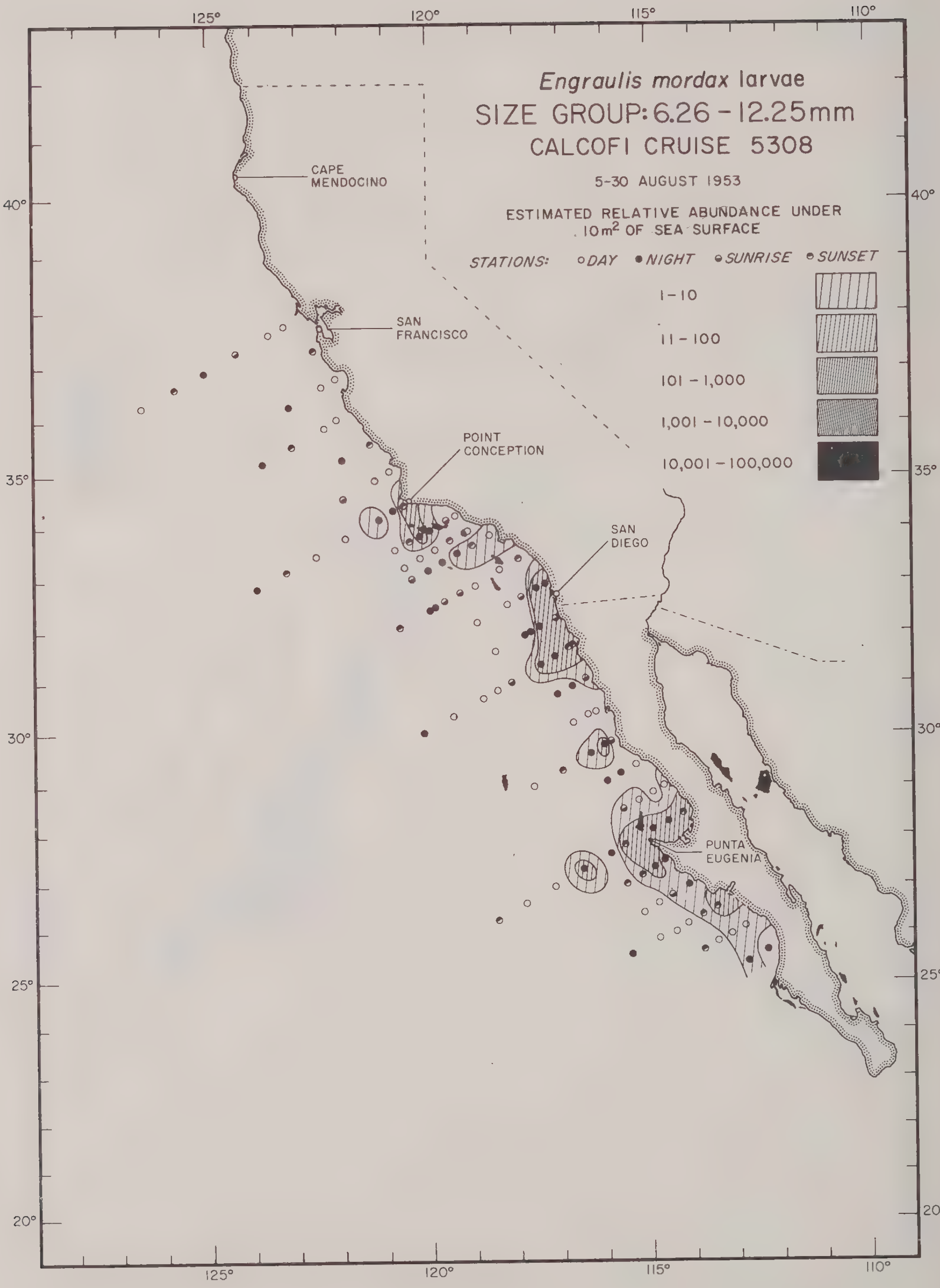
5307


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5307
8-27 JULY 1953
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◐SUNRISE ◑SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

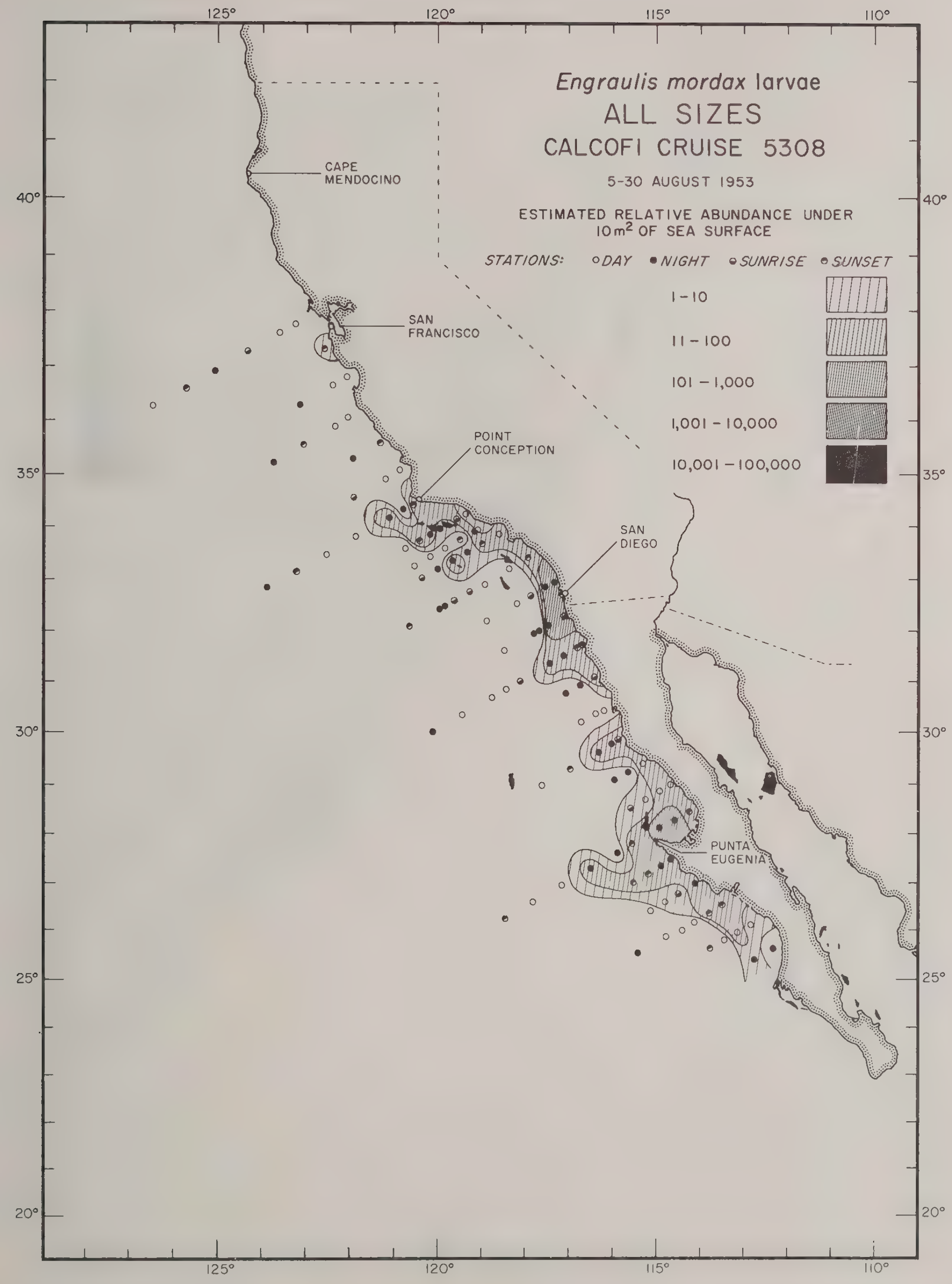
5307


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5308
5-30 AUGUST 1953
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

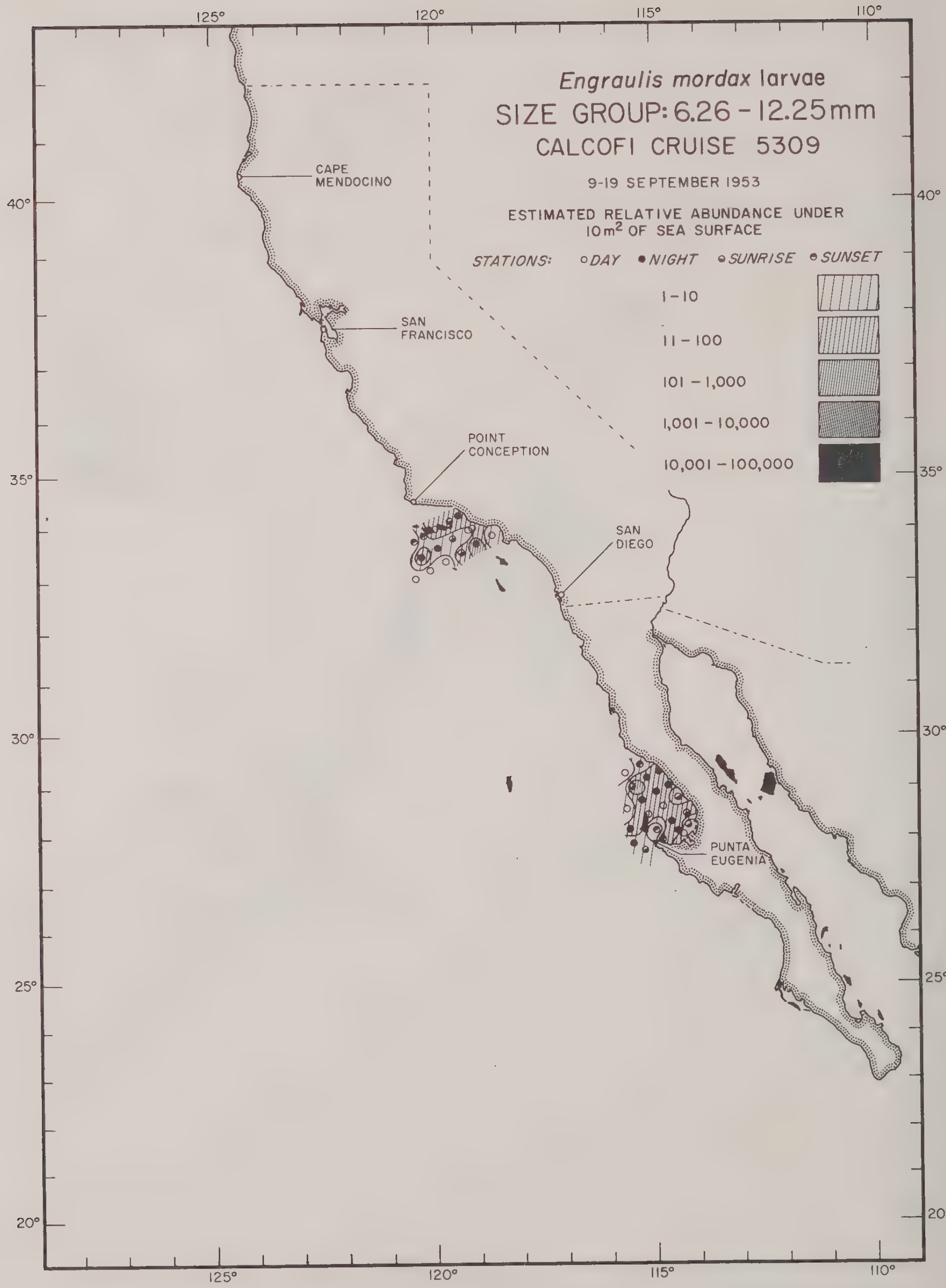
5308


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5308
5-30 AUGUST 1953
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

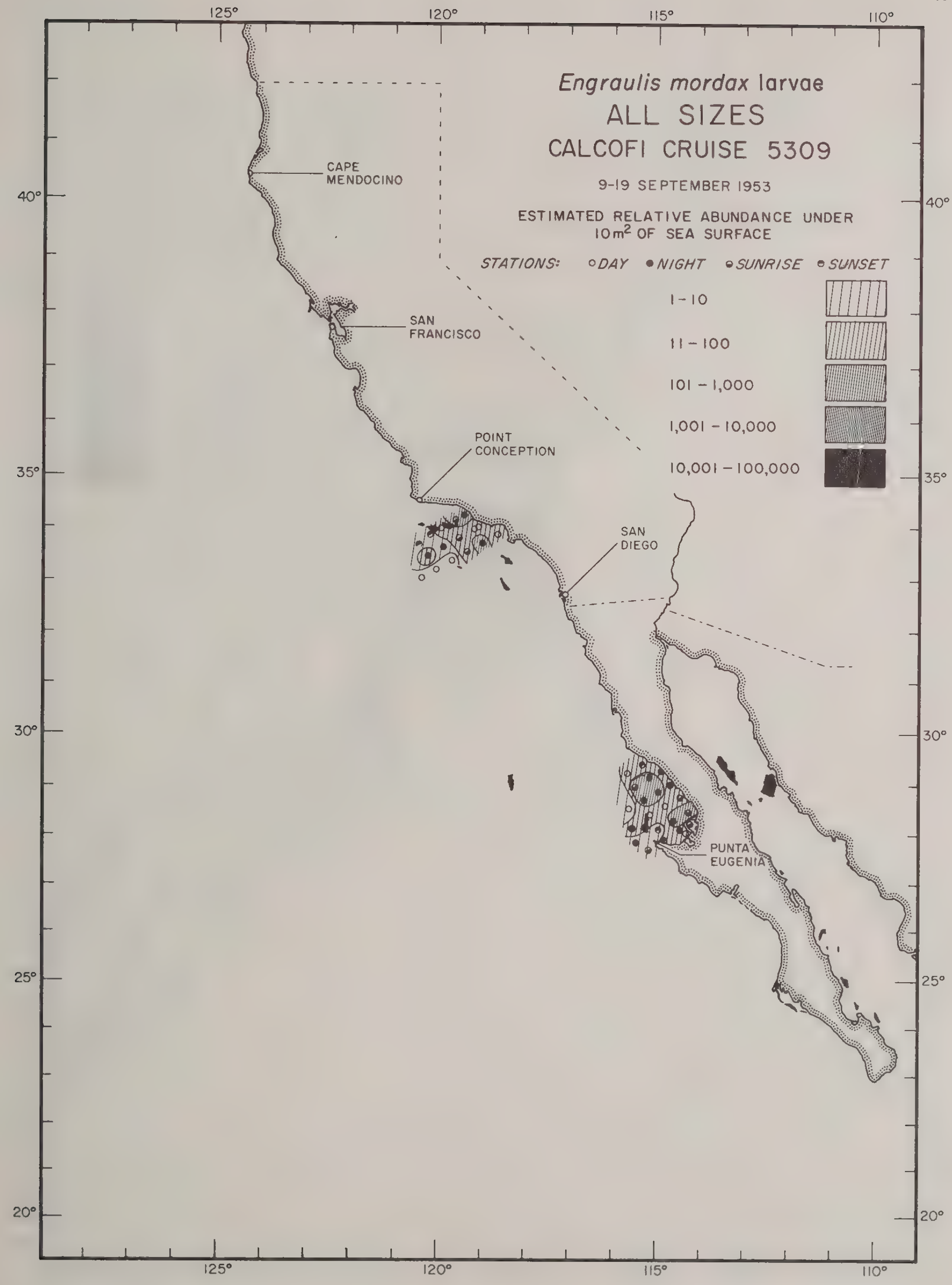
5308


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5309
9-19 SEPTEMBER 1953
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◉ SUNRISE ◉ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

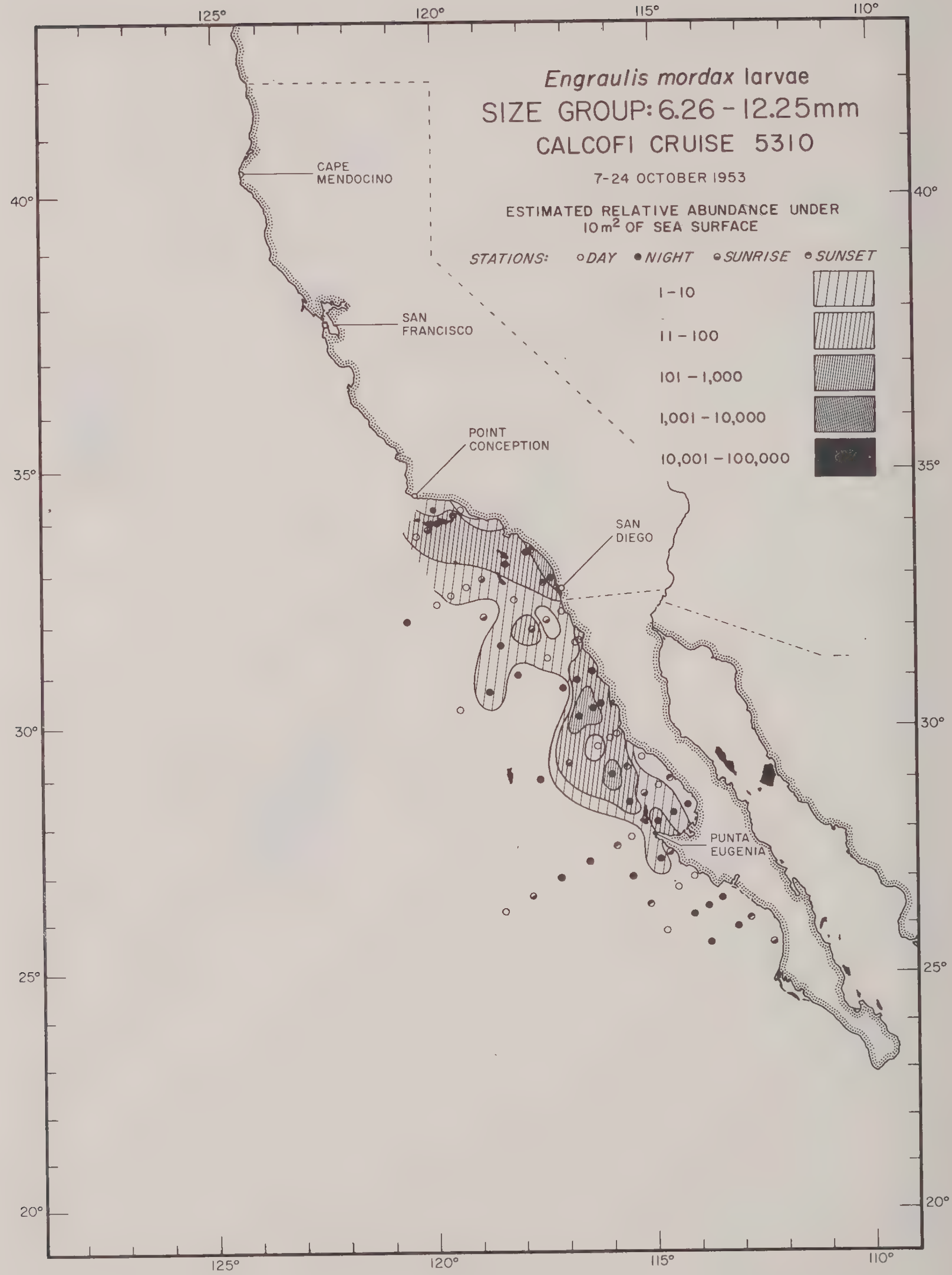
Size Group: 6.26-12.25mm

5309


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5309
9-19 SEPTEMBER 1953
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

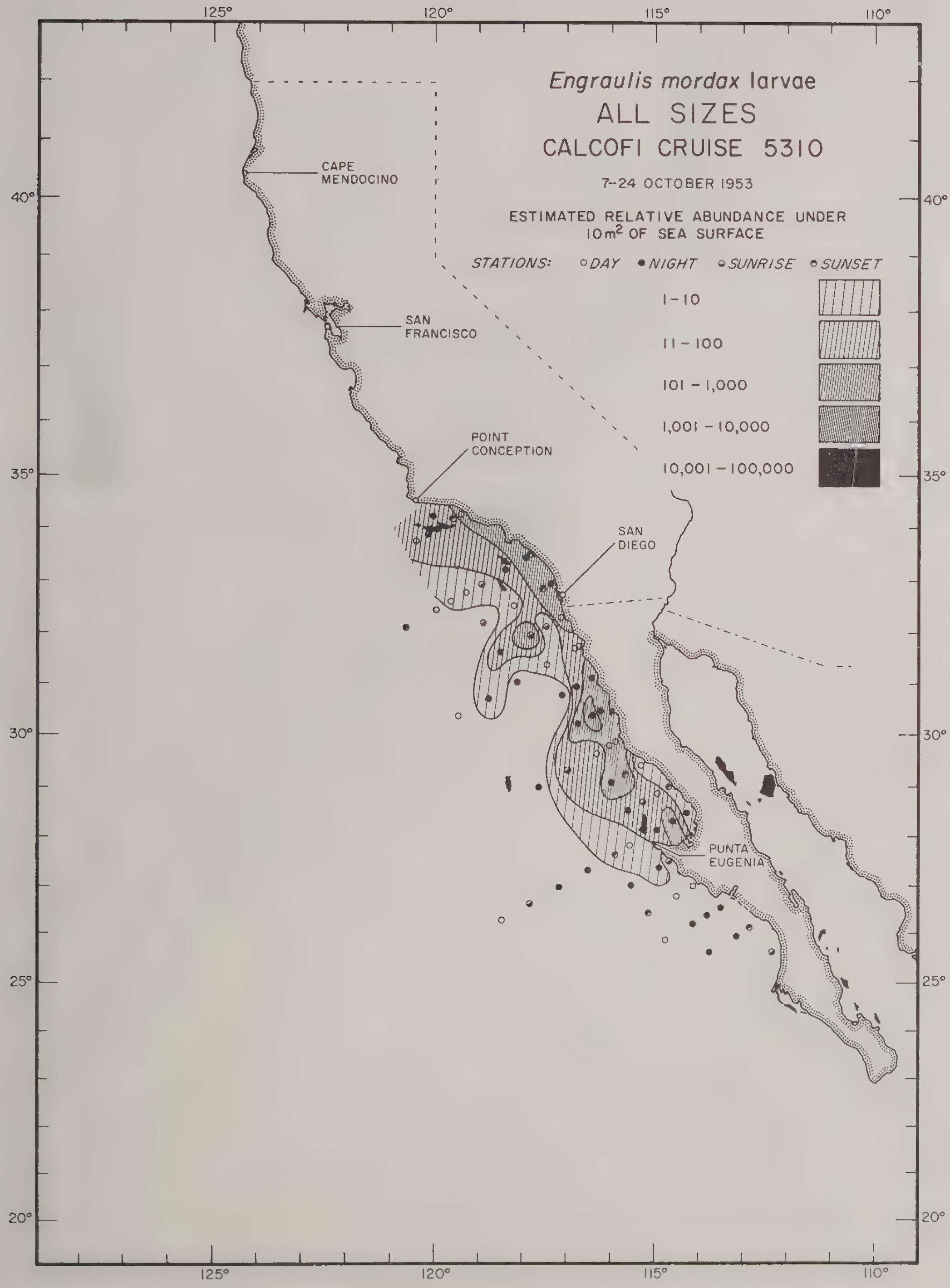
All Sizes
5309


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5310
7-24 OCTOBER 1953
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◉ SUNRISE ◉ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

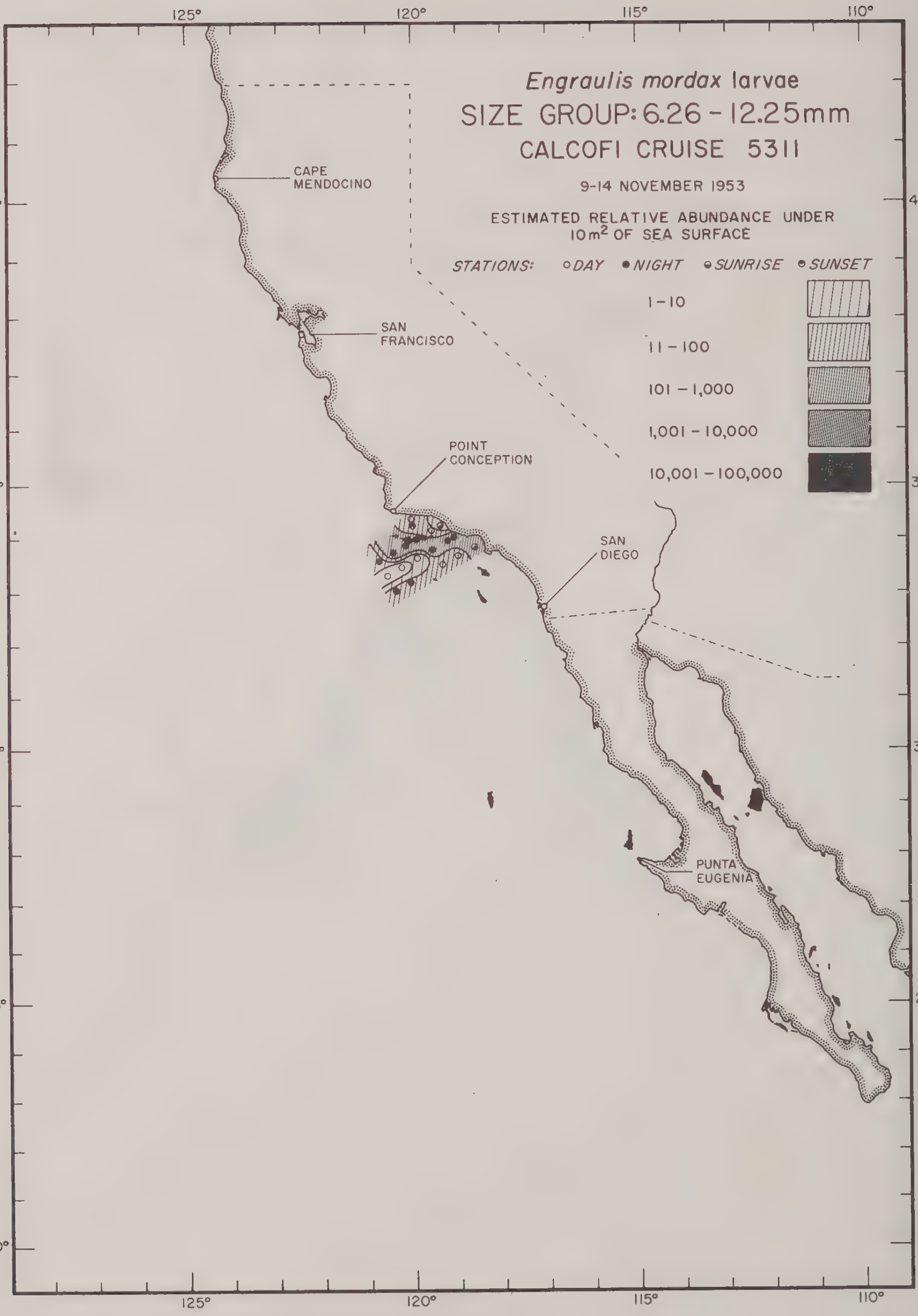
5310


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5310
7-24 OCTOBER 1953
ESTIMATED RELATIVE ABUNDANCE UNDER
$10 m^2$ OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

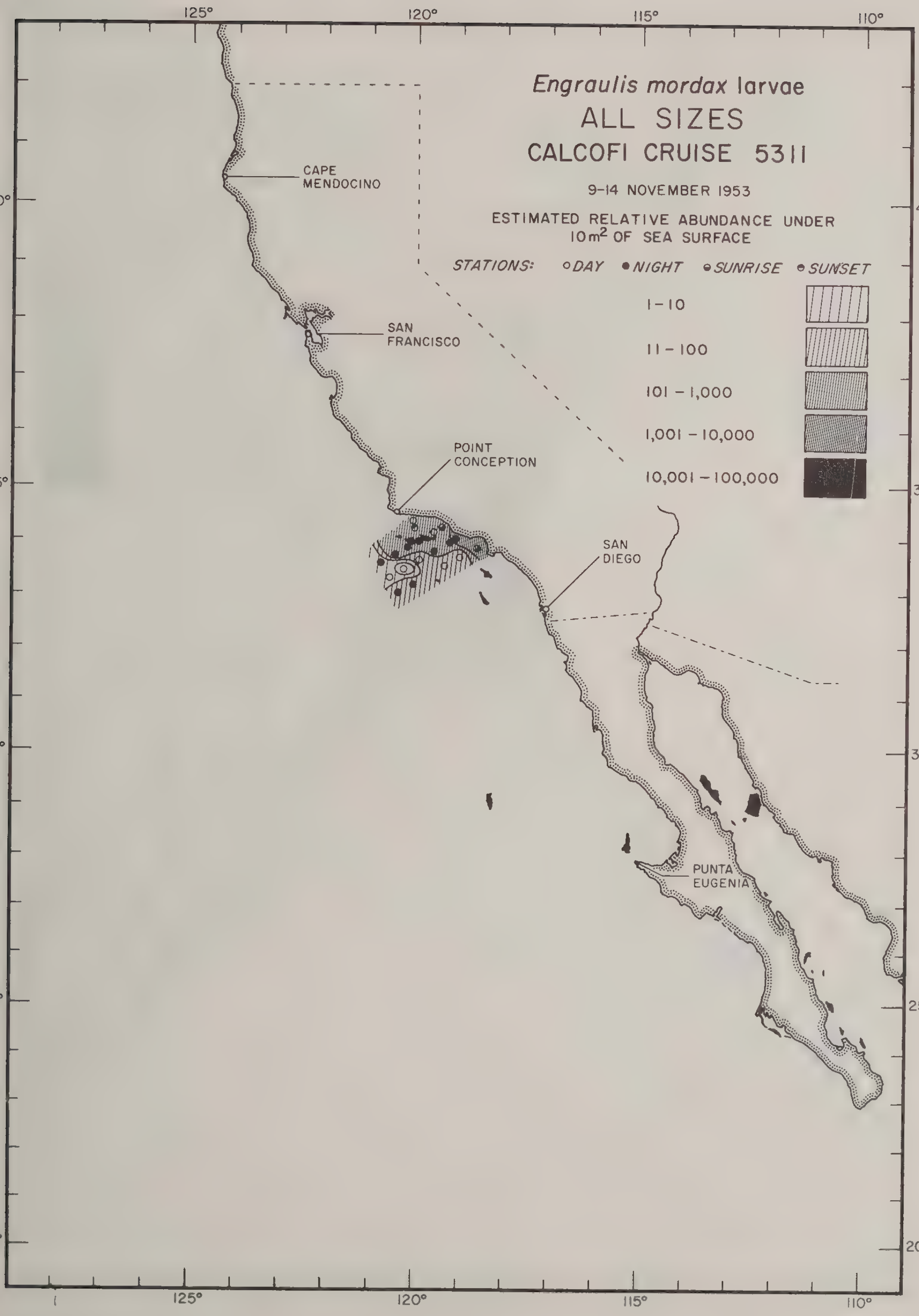
5310


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5311
9-14 NOVEMBER 1953
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

5311

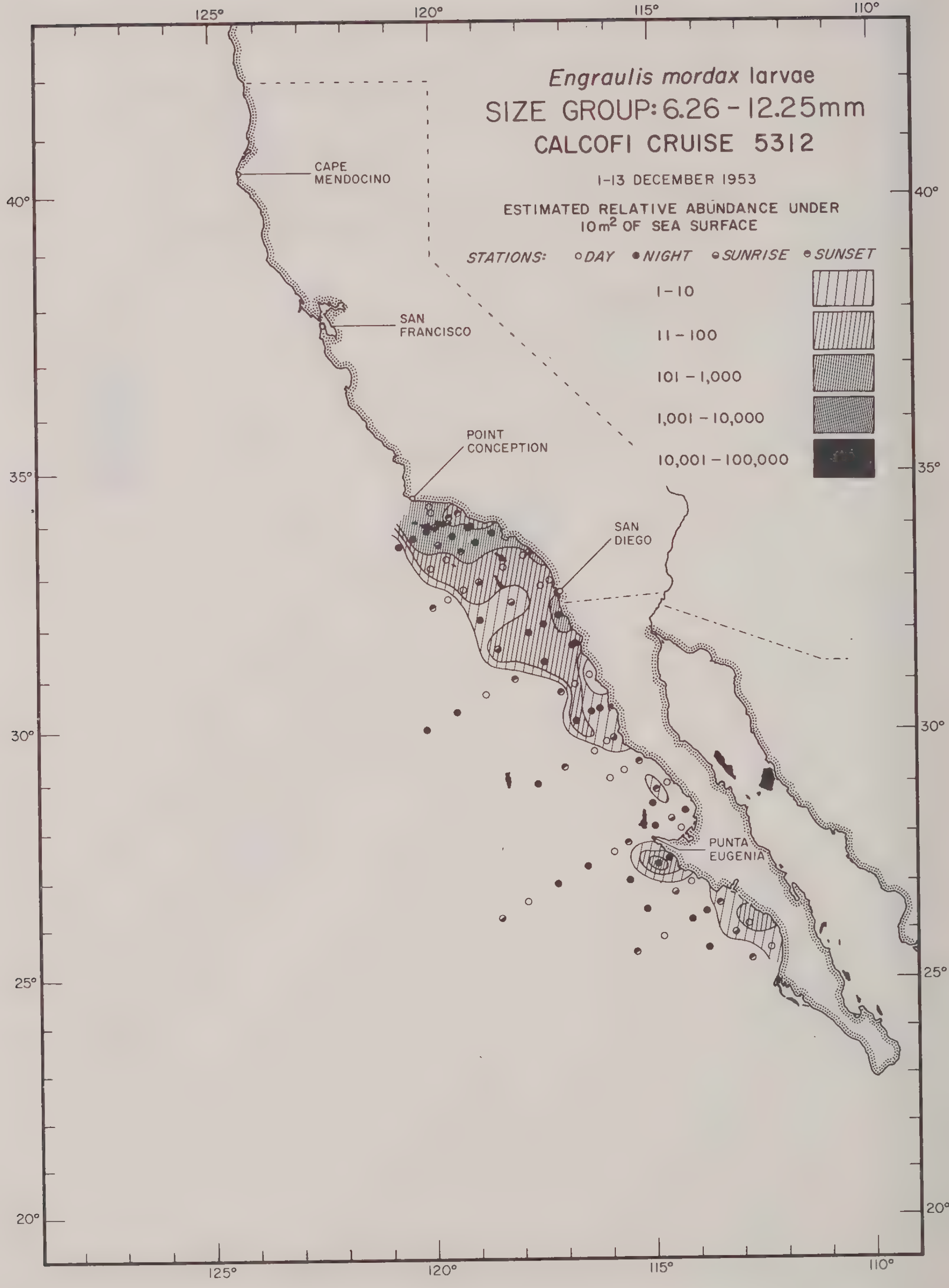


125°
120°
115°
110°
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5311
9-14 NOVEMBER 1953
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◉ SUNRISE ◉ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

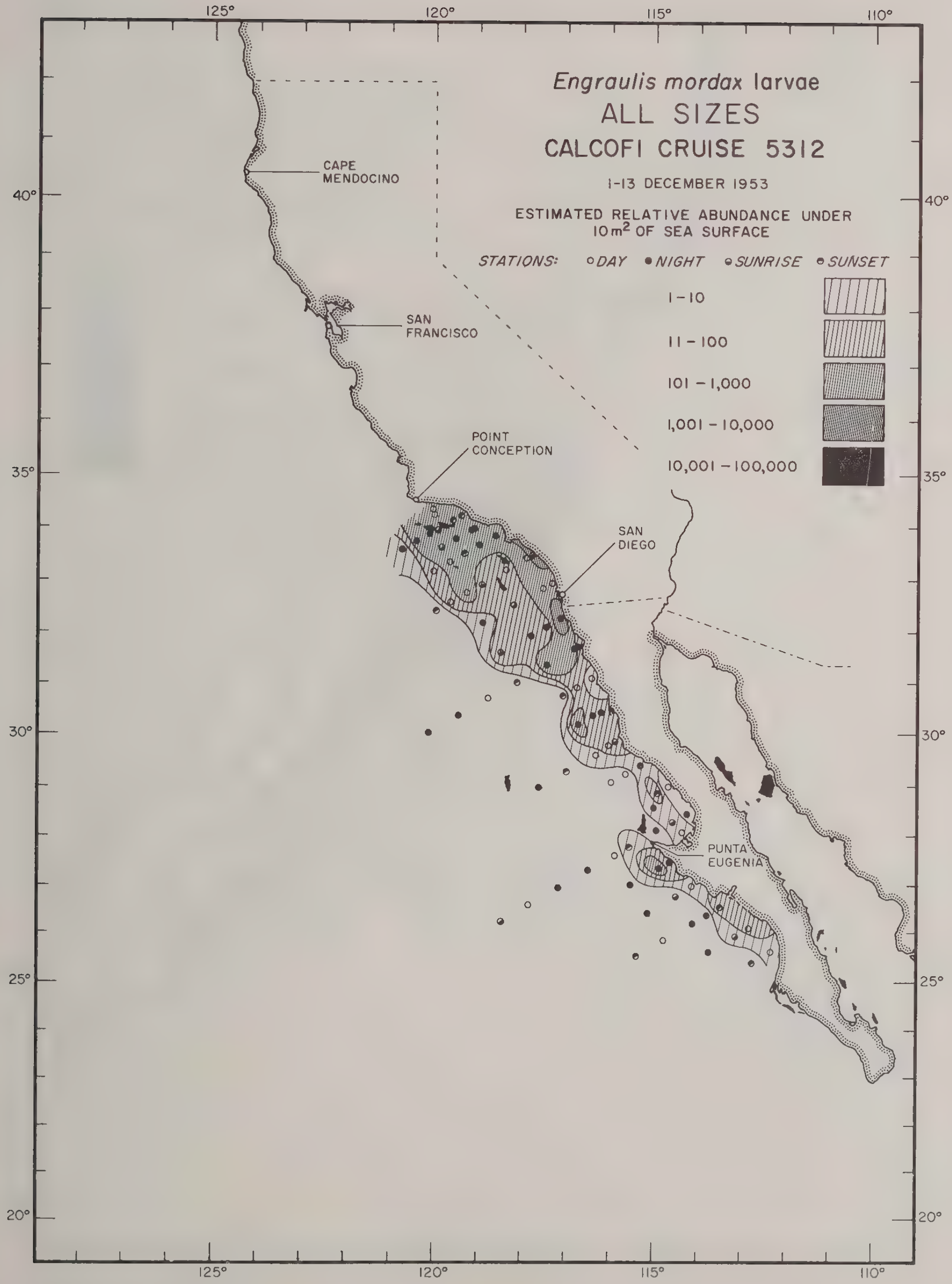
5311


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5312
1-13 DECEMBER 1953
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○ *DAY* ● *NIGHT* ◒ *SUNRISE* ◓ *SUNSET*
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

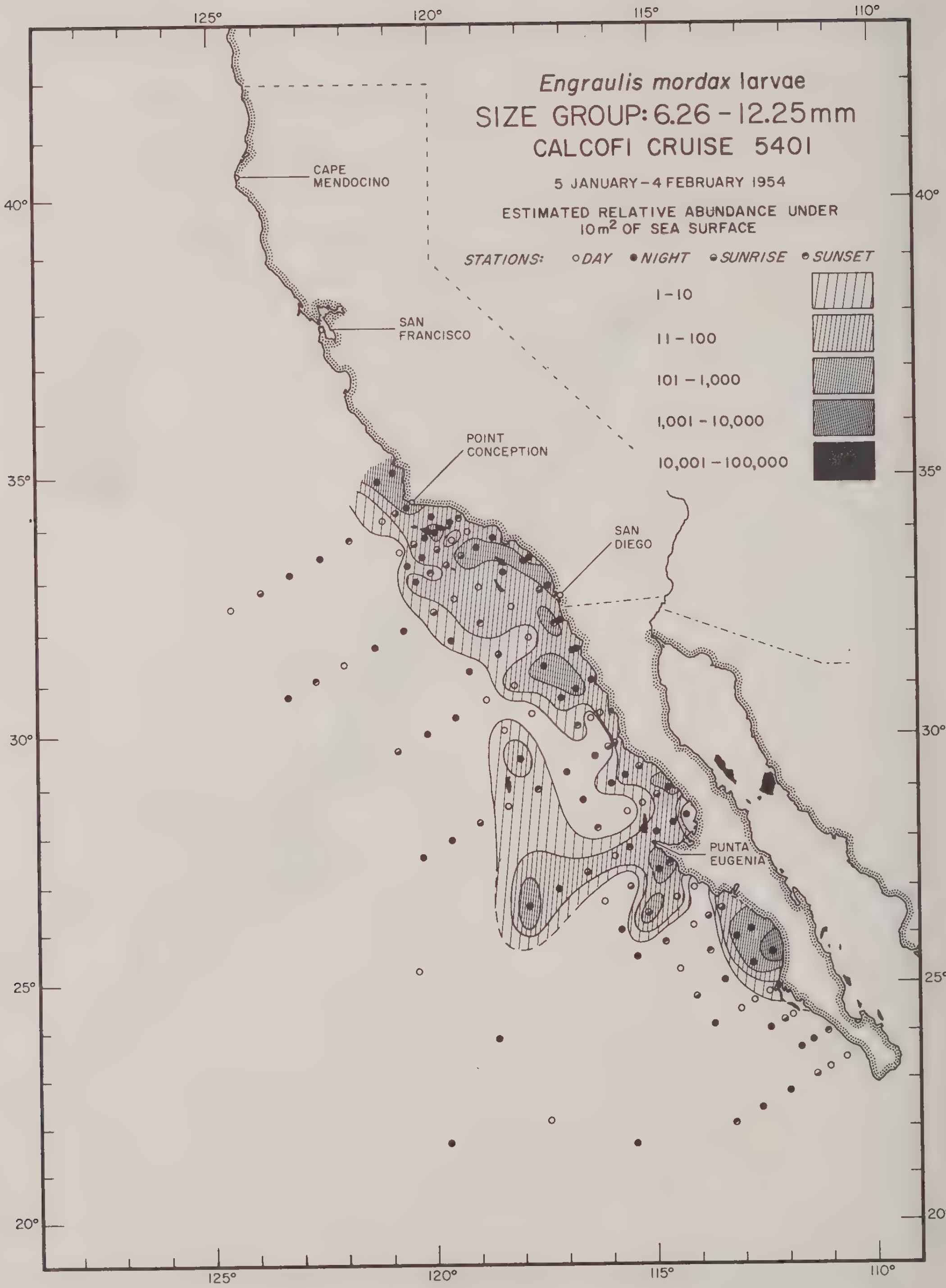
5312


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5312
1-13 DECEMBER 1953
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

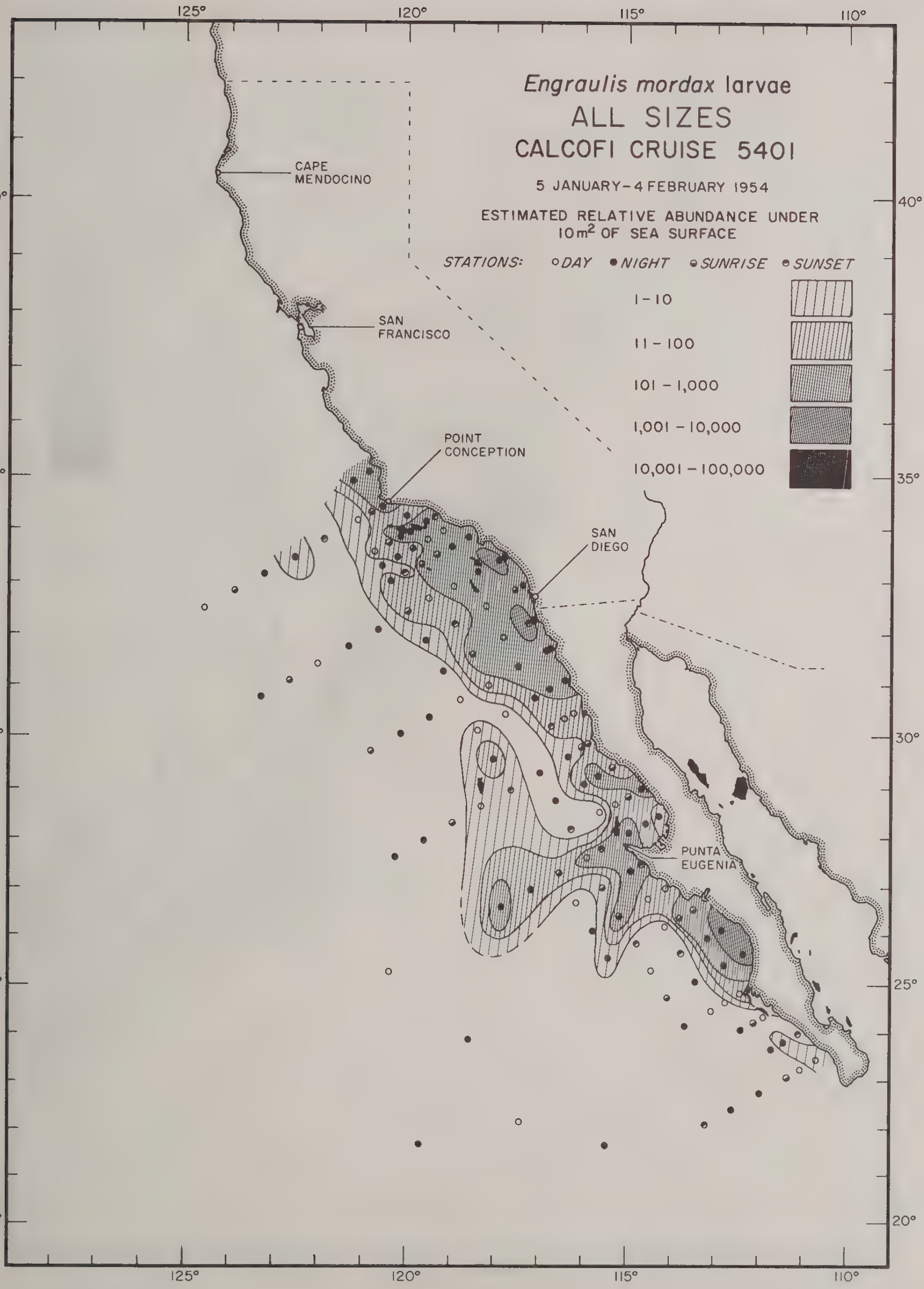
5312


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5401
5 JANUARY - 4 FEBRUARY 1954
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

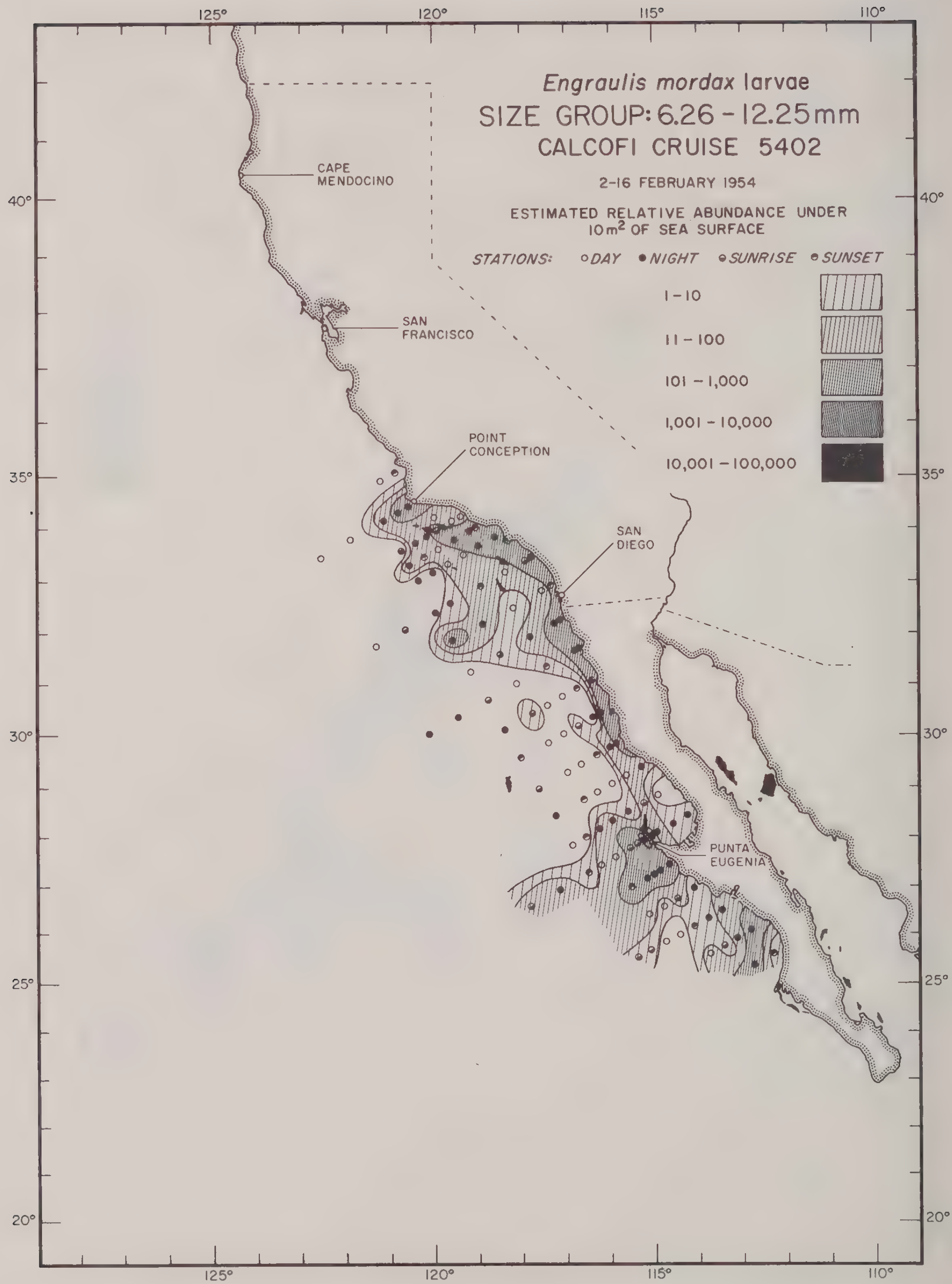
5401


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5401
5 JANUARY–4 FEBRUARY 1954
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1–10
11–100
101–1,000
1,001–10,000
10,001–100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

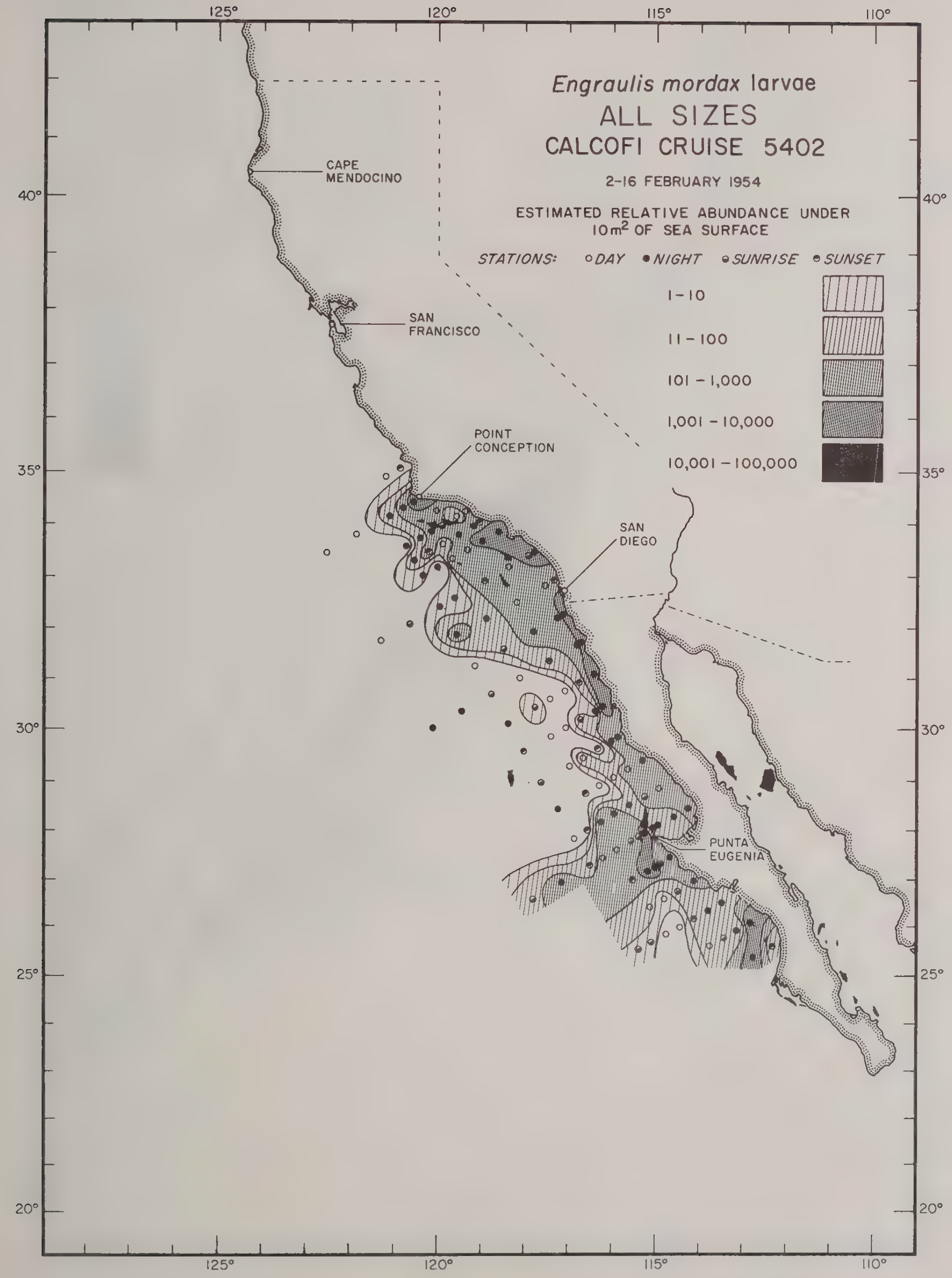
5401


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5402
2-16 FEBRUARY 1954
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◉ SUNRISE ◉ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

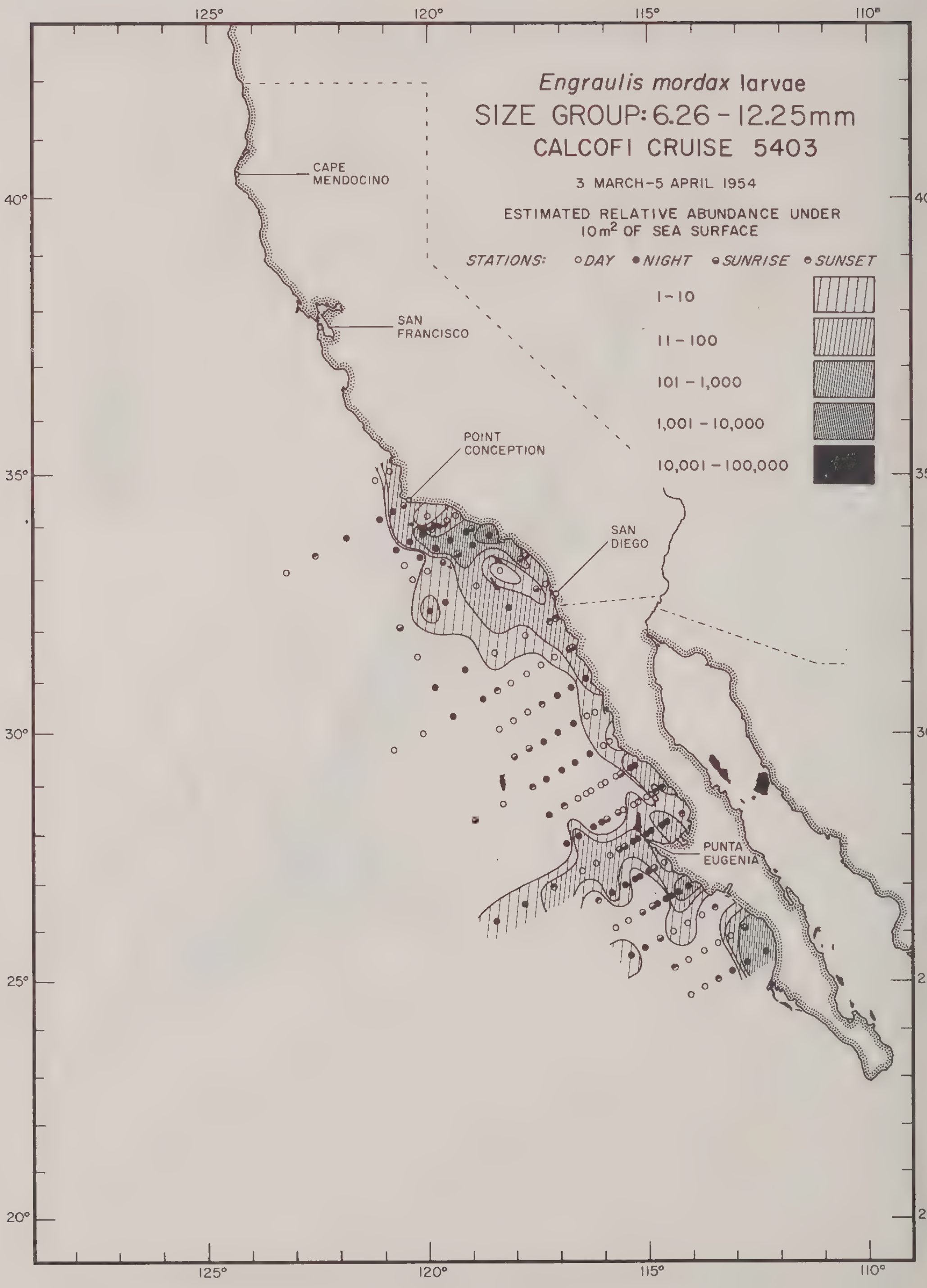
5402


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5402
2-16 FEBRUARY 1954
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

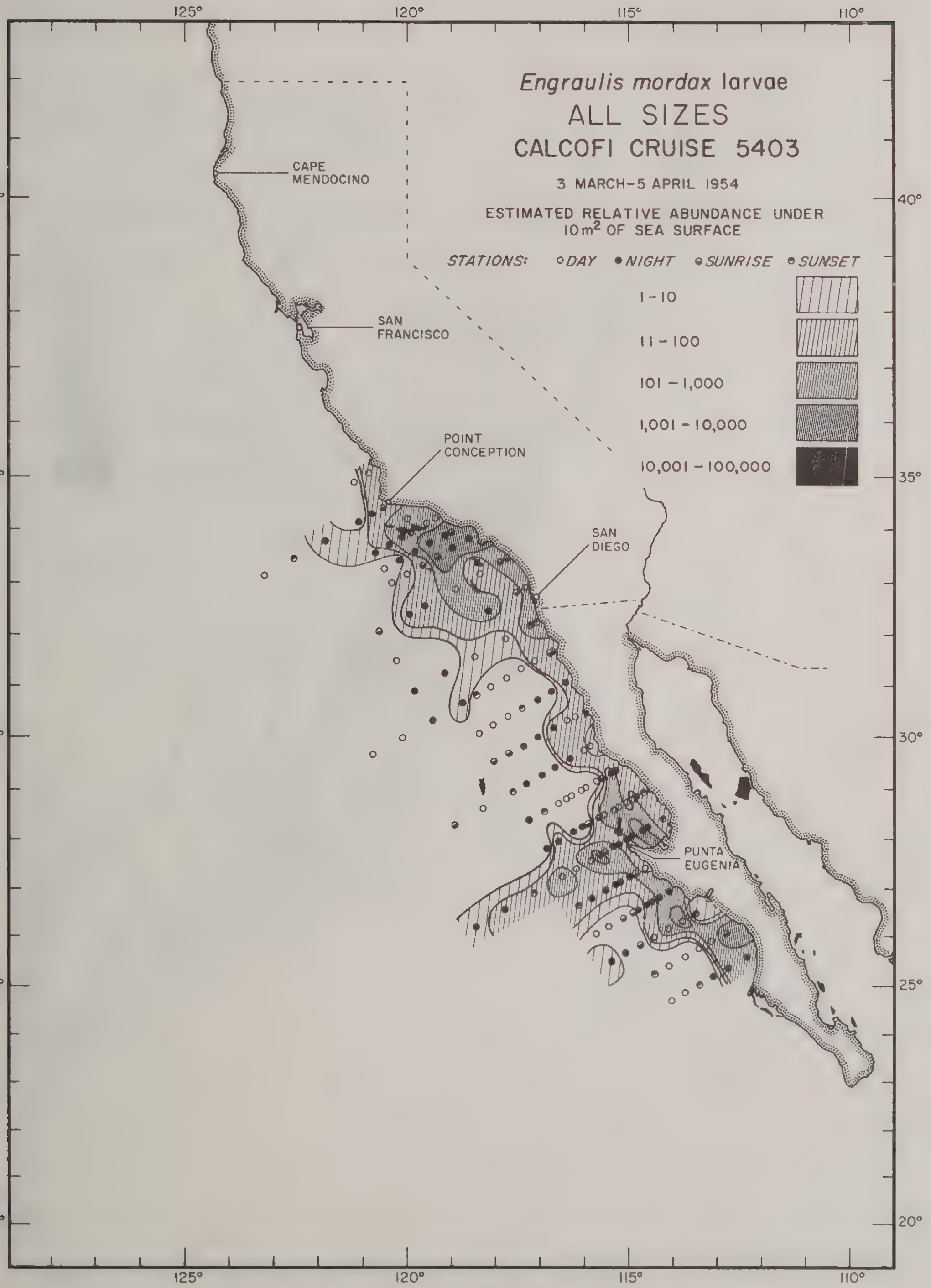
5402


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5403
3 MARCH-5 APRIL 1954
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

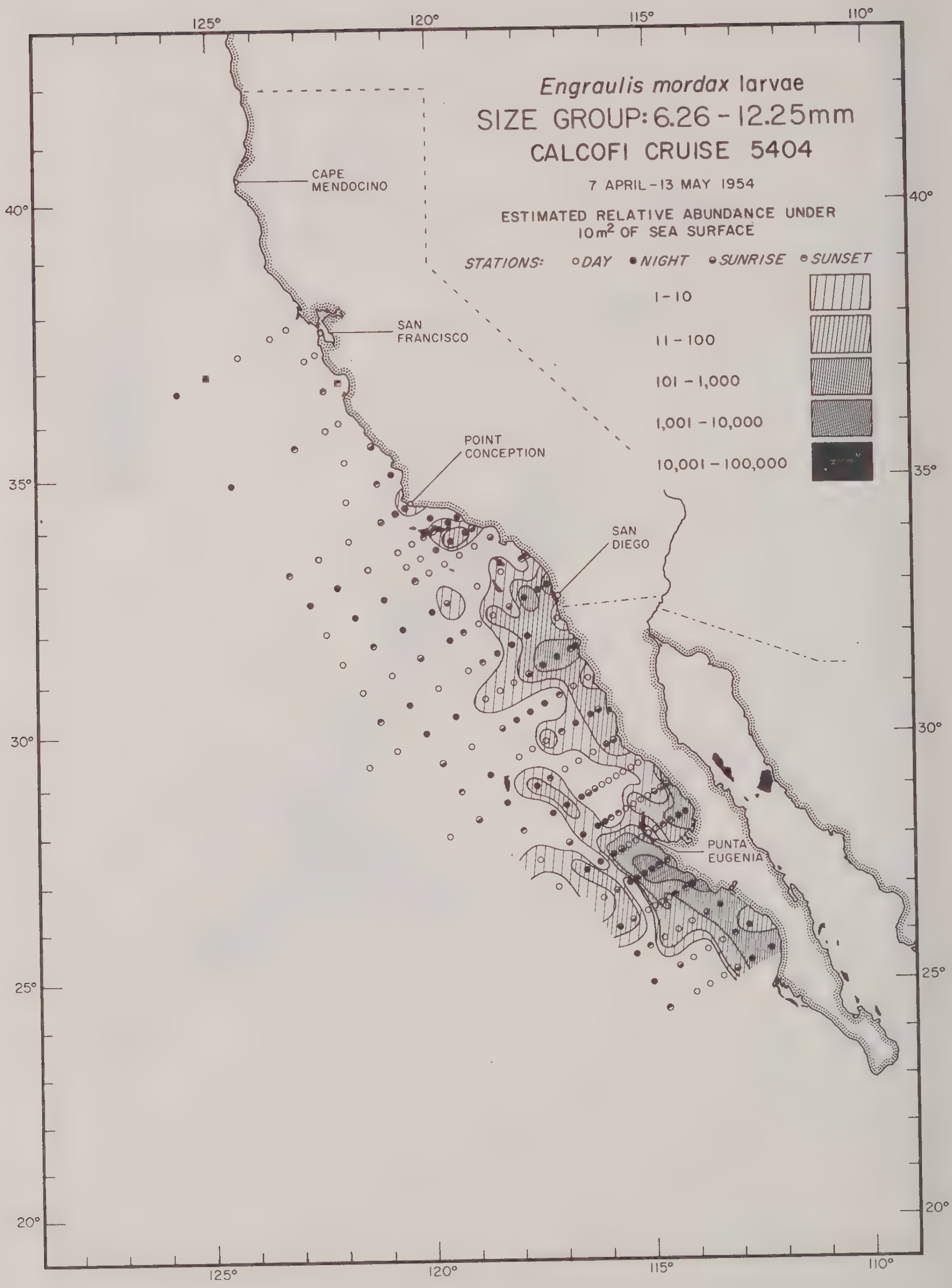
5403


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5403
3 MARCH–5 APRIL 1954
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

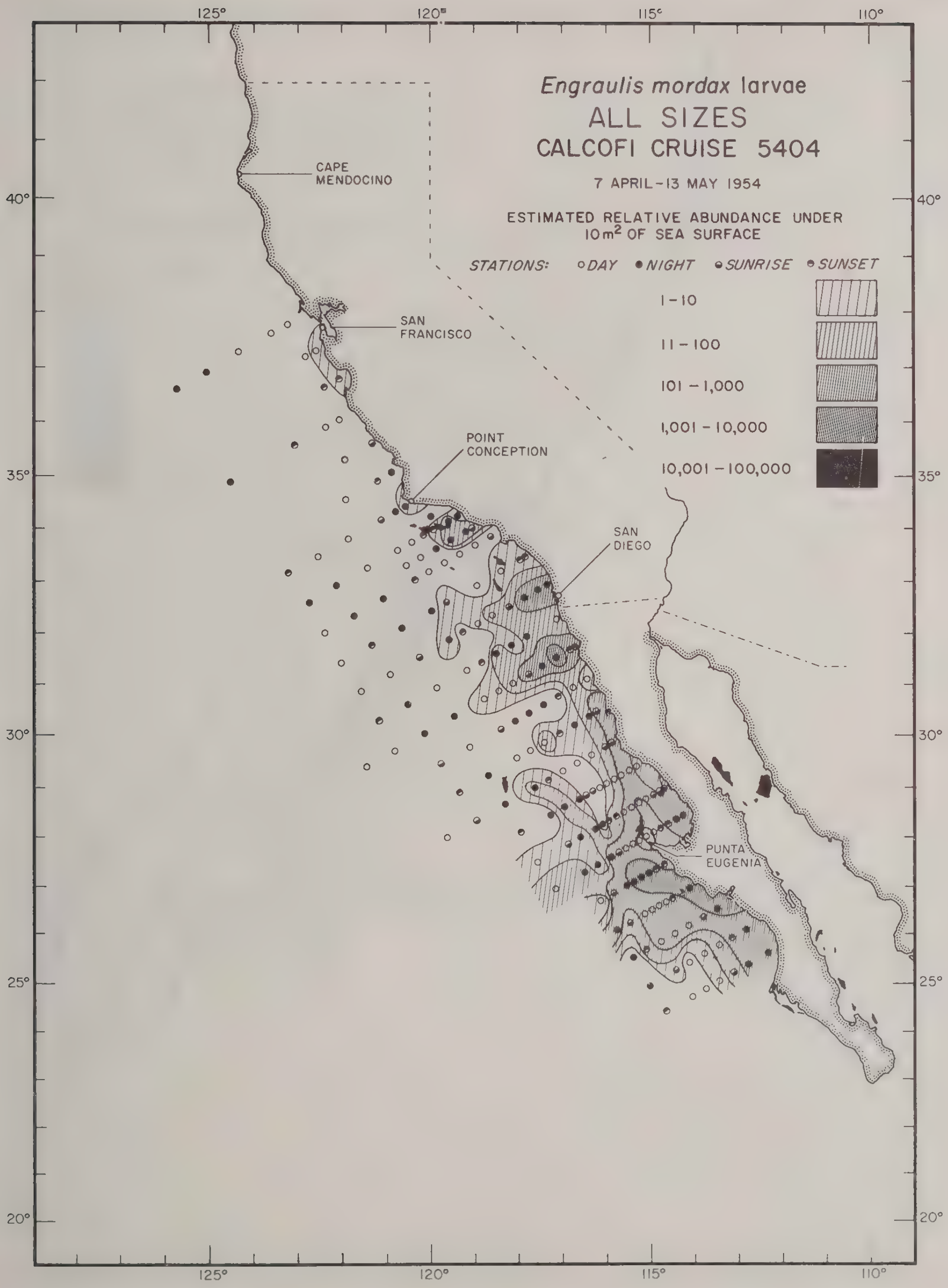
5403


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5404
7 APRIL - 13 MAY 1954
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

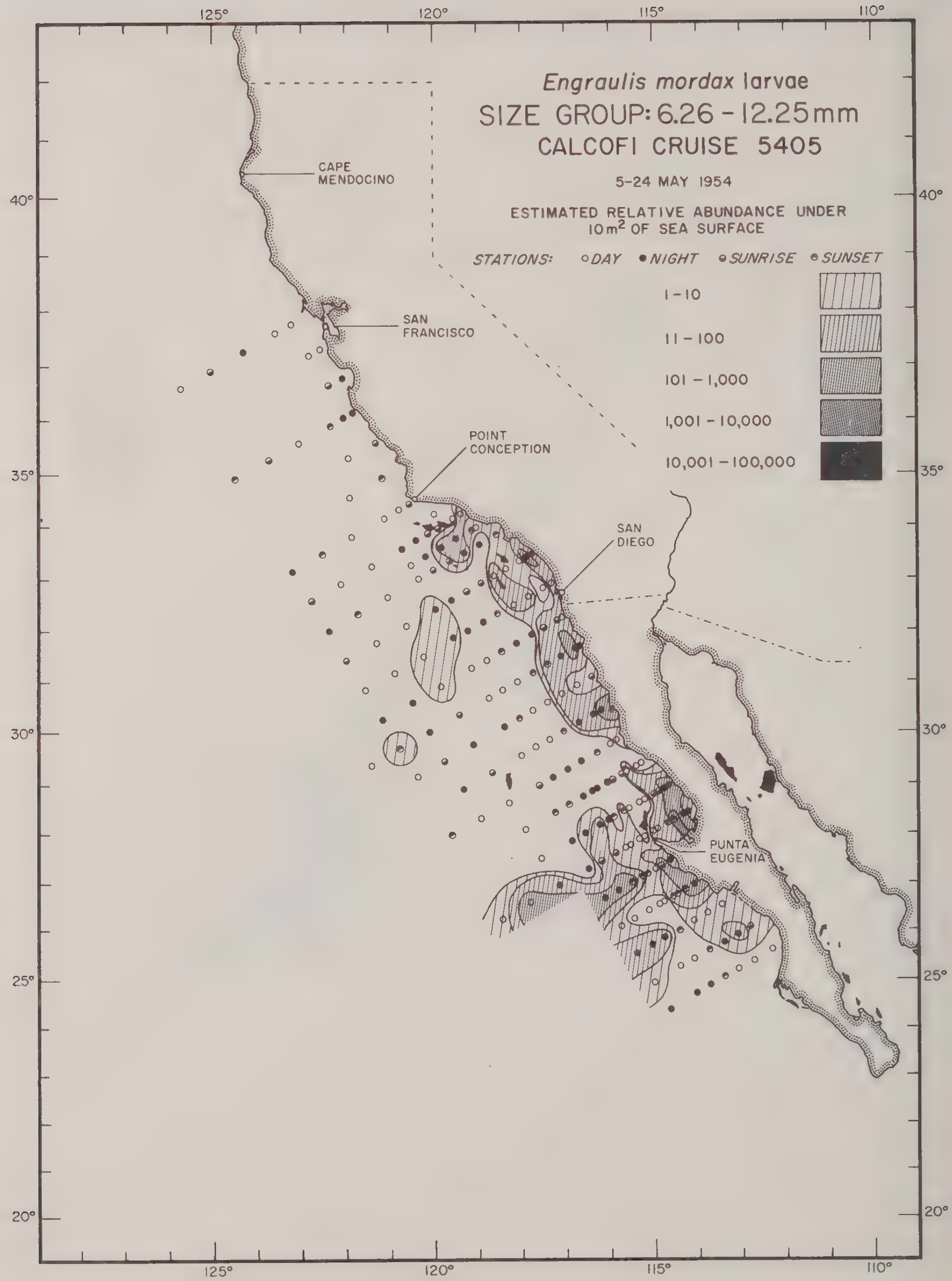
5404


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5404
7 APRIL-13 MAY 1954
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

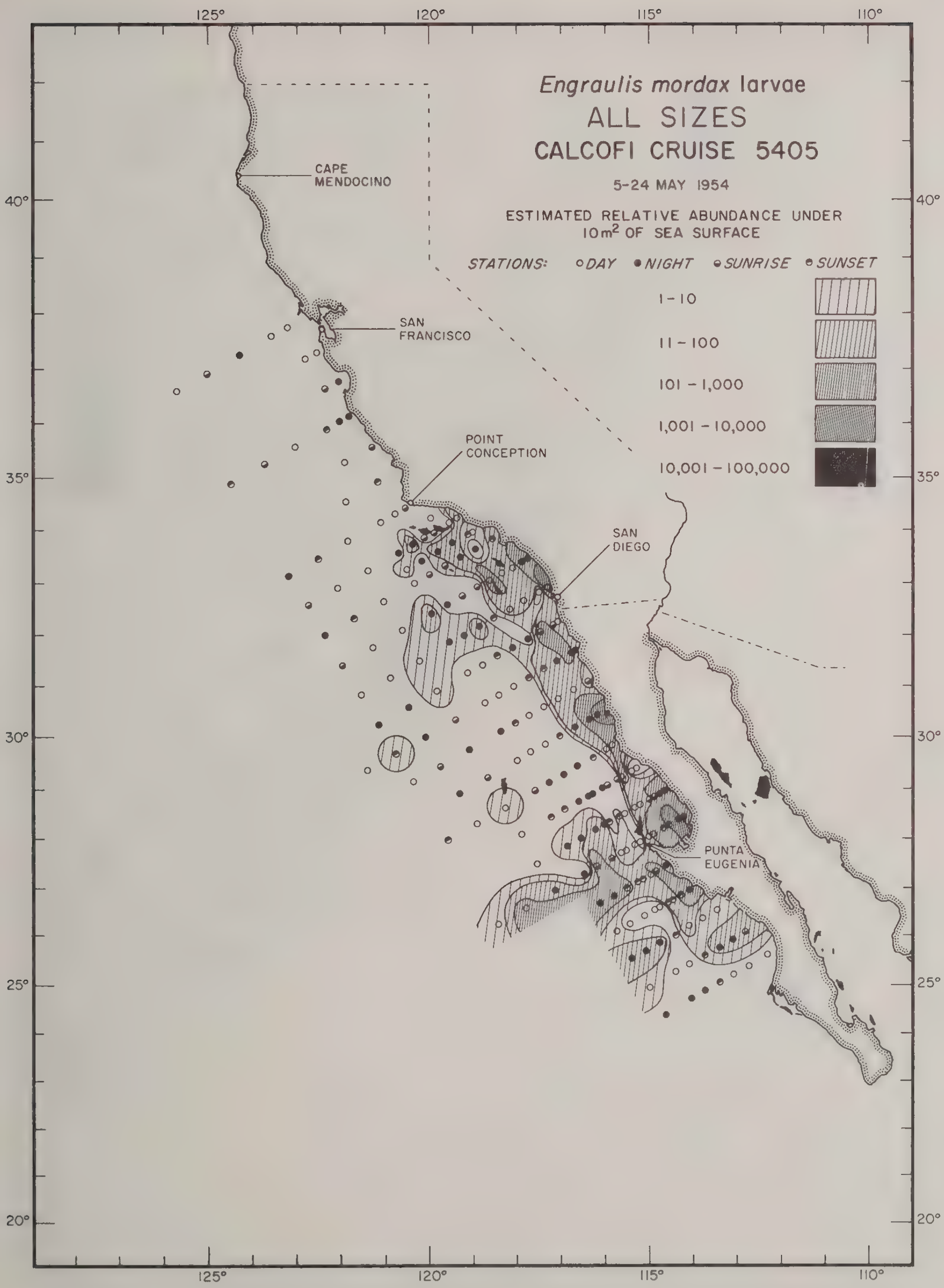
5404


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5405
5-24 MAY 1954
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ *DAY* ● *NIGHT* ◒ *SUNRISE* ◓ *SUNSET*
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

Size Group: 6.26-12.25mm

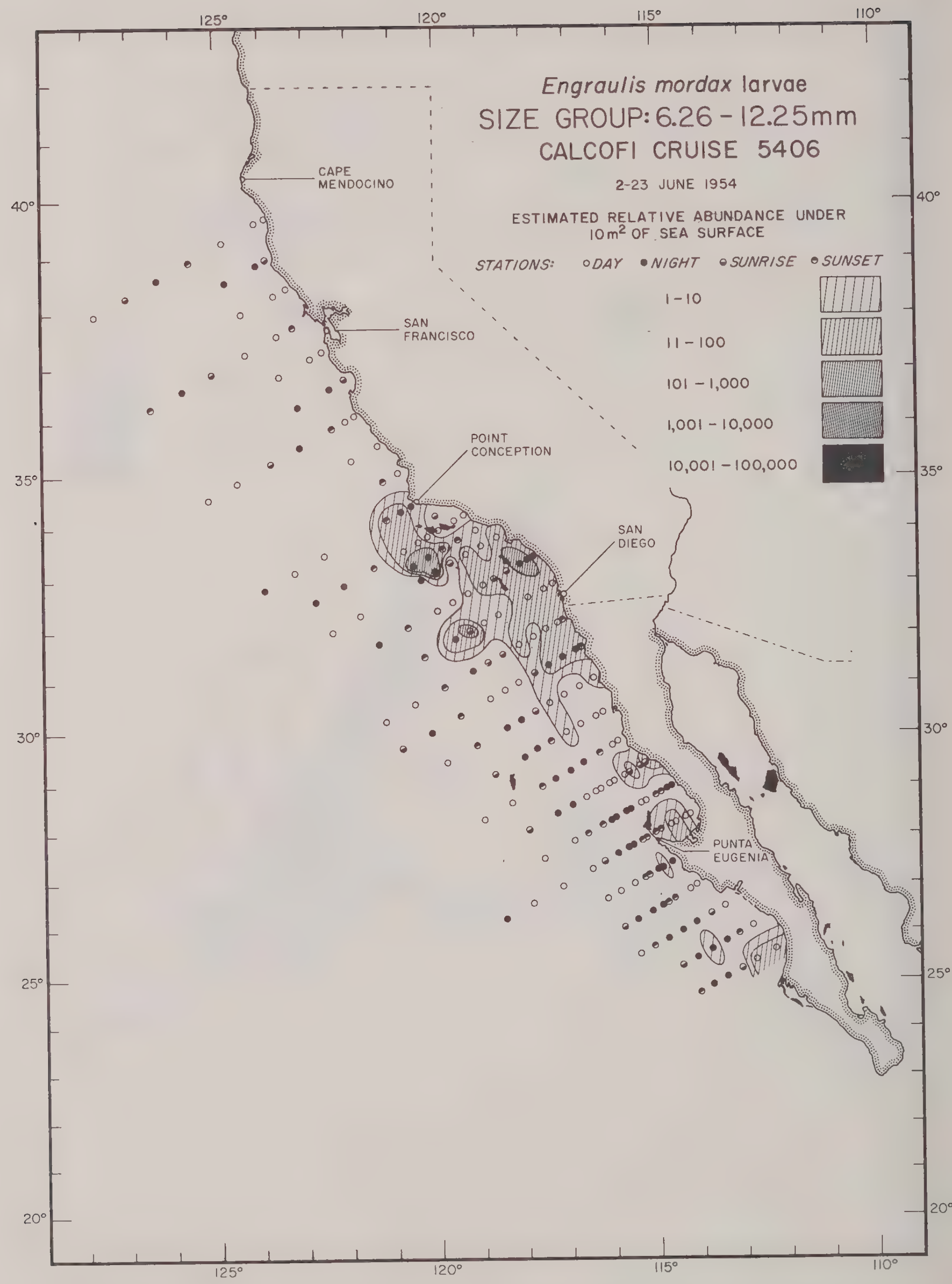
5405


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5405
5-24 MAY 1954
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

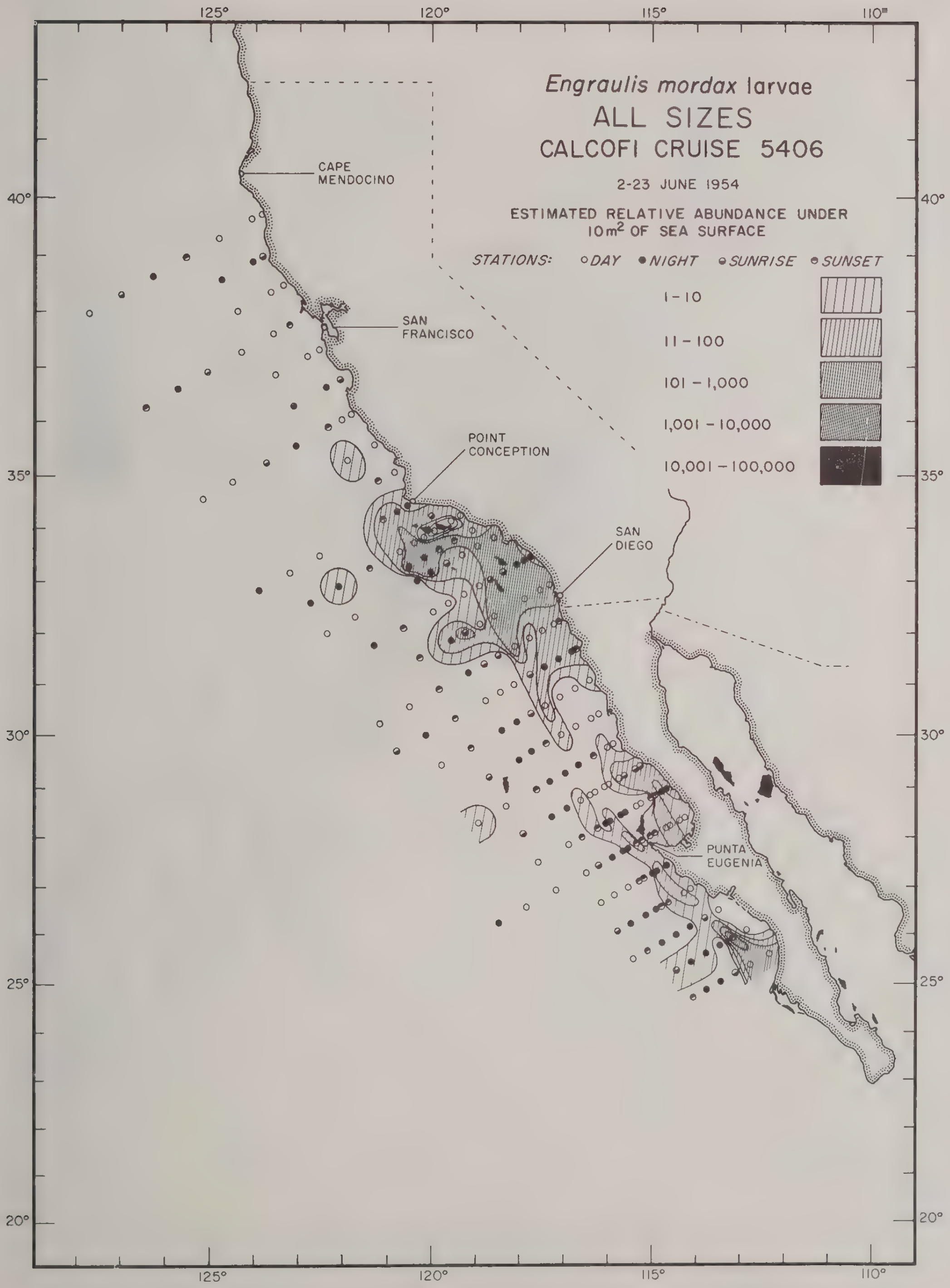
5405


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5406
2-23 JUNE 1954
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

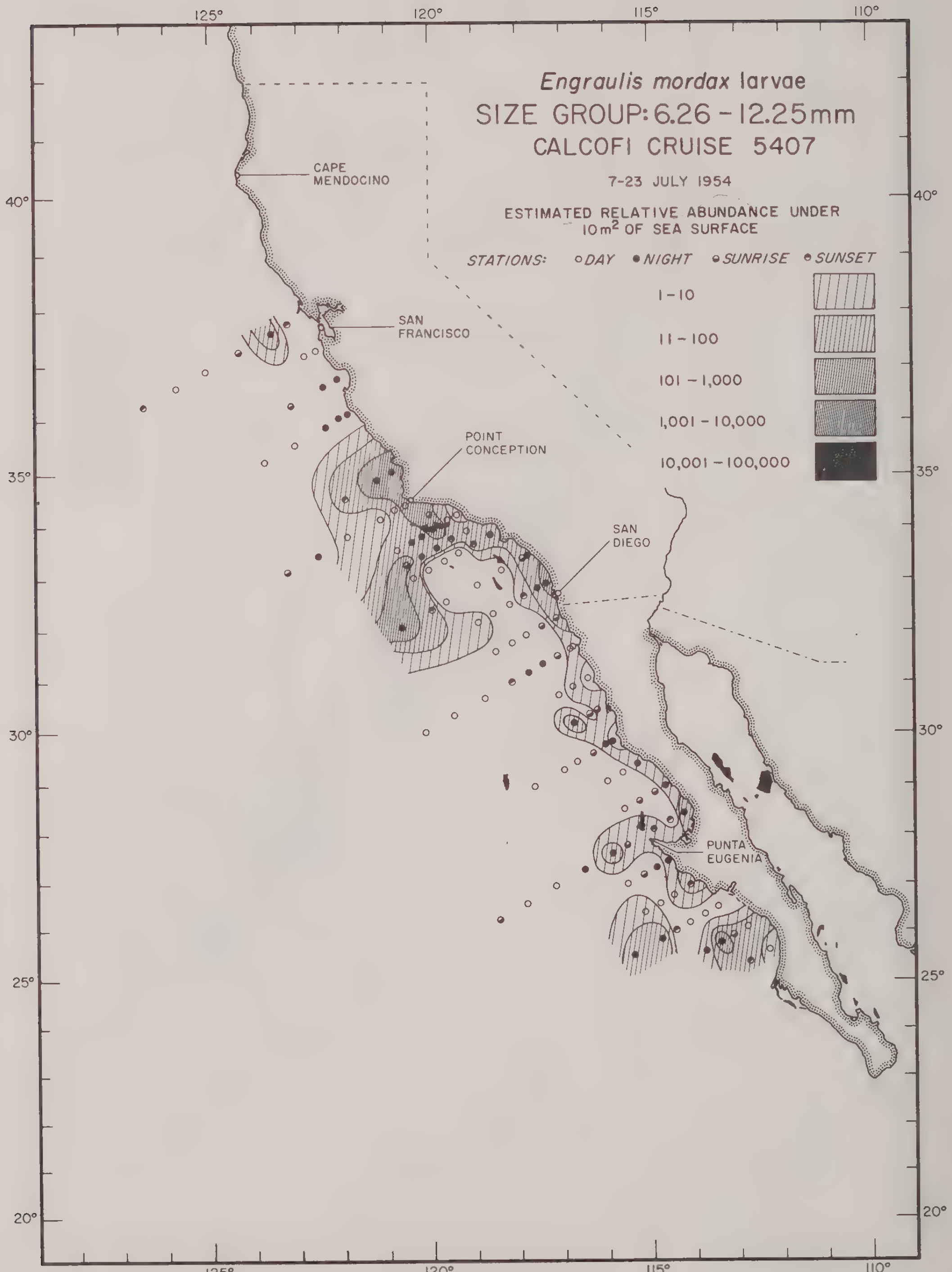
Size Group: 6.26-12.25mm

5406


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5406
2-23 JUNE 1954
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes
5406

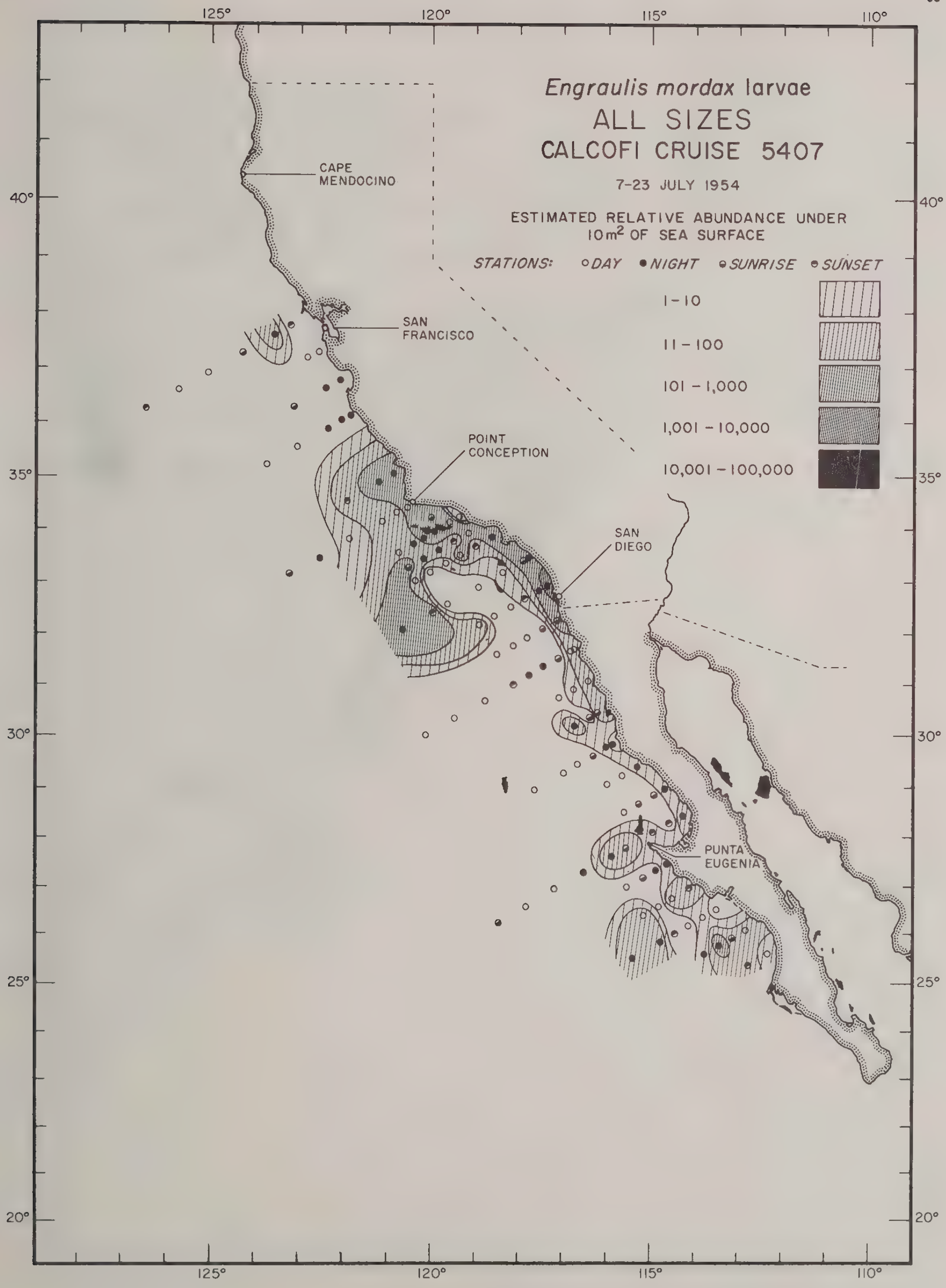


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5407
7-23 JULY 1954
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ *DAY* ● *NIGHT* ◐ *SUNRISE* ◑ *SUNSET*
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

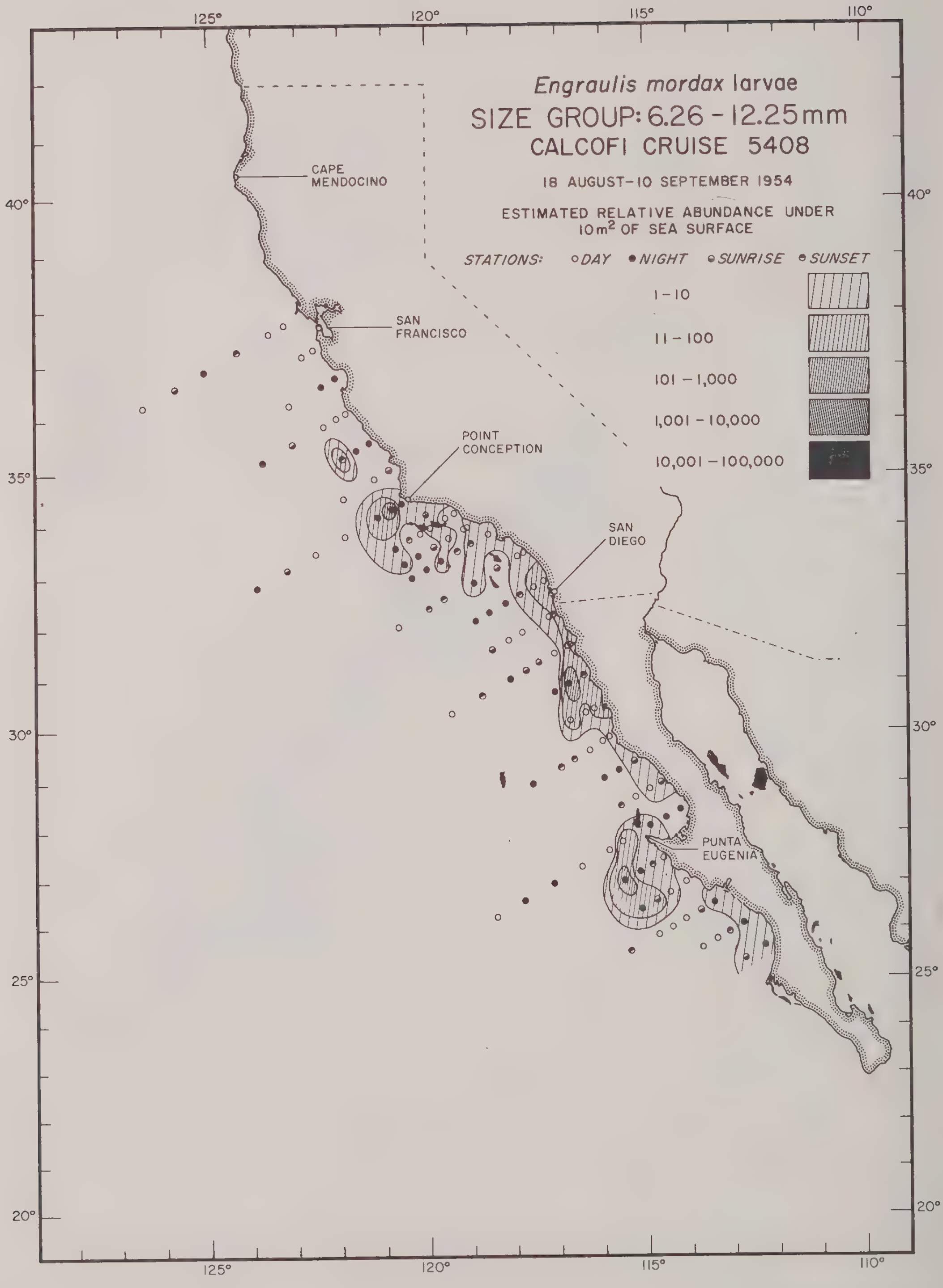
5407


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5407
7-23 JULY 1954
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

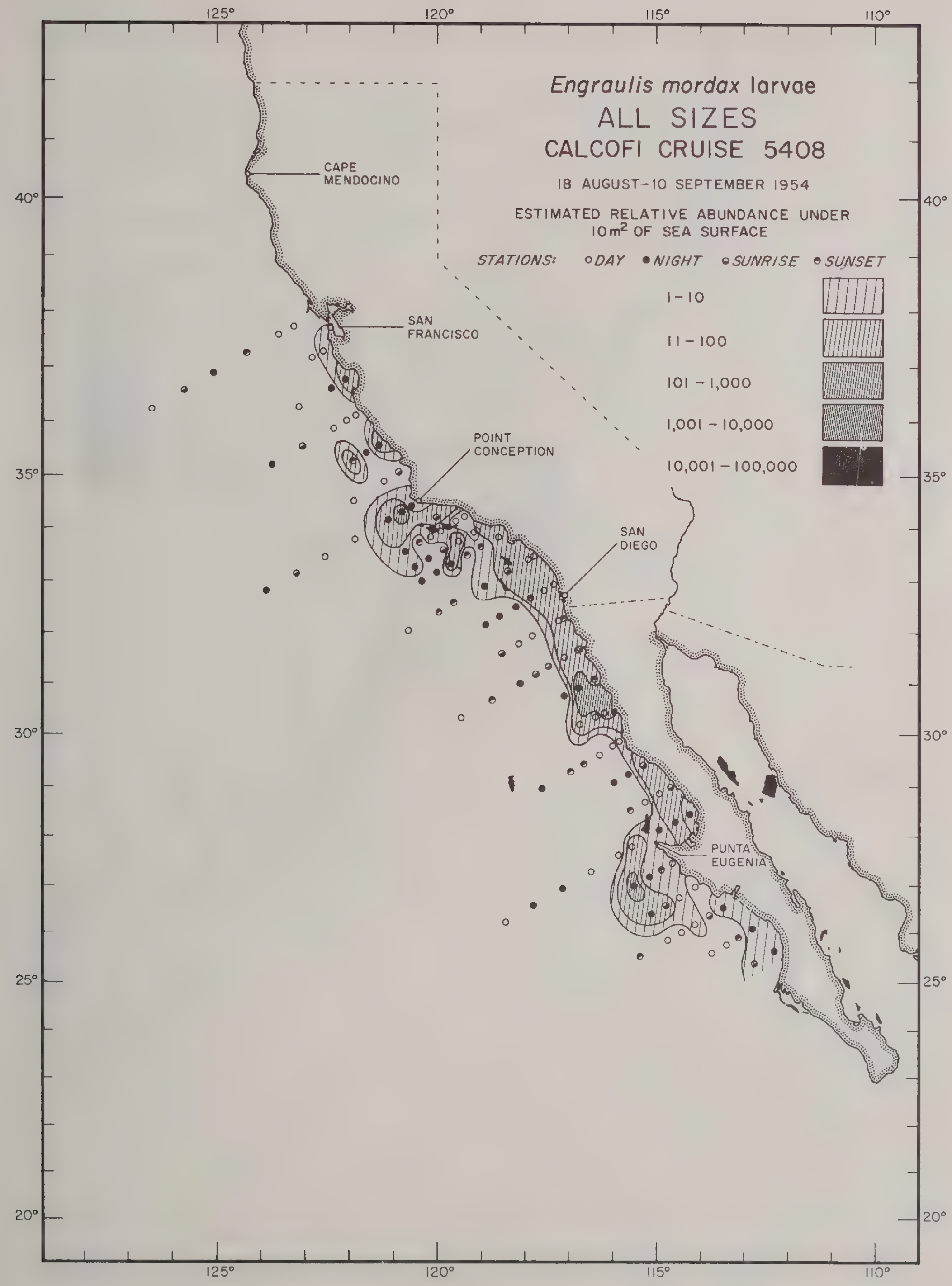
5407


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5408
18 AUGUST-10 SEPTEMBER 1954
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ⊖ SUNRISE ⊕ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

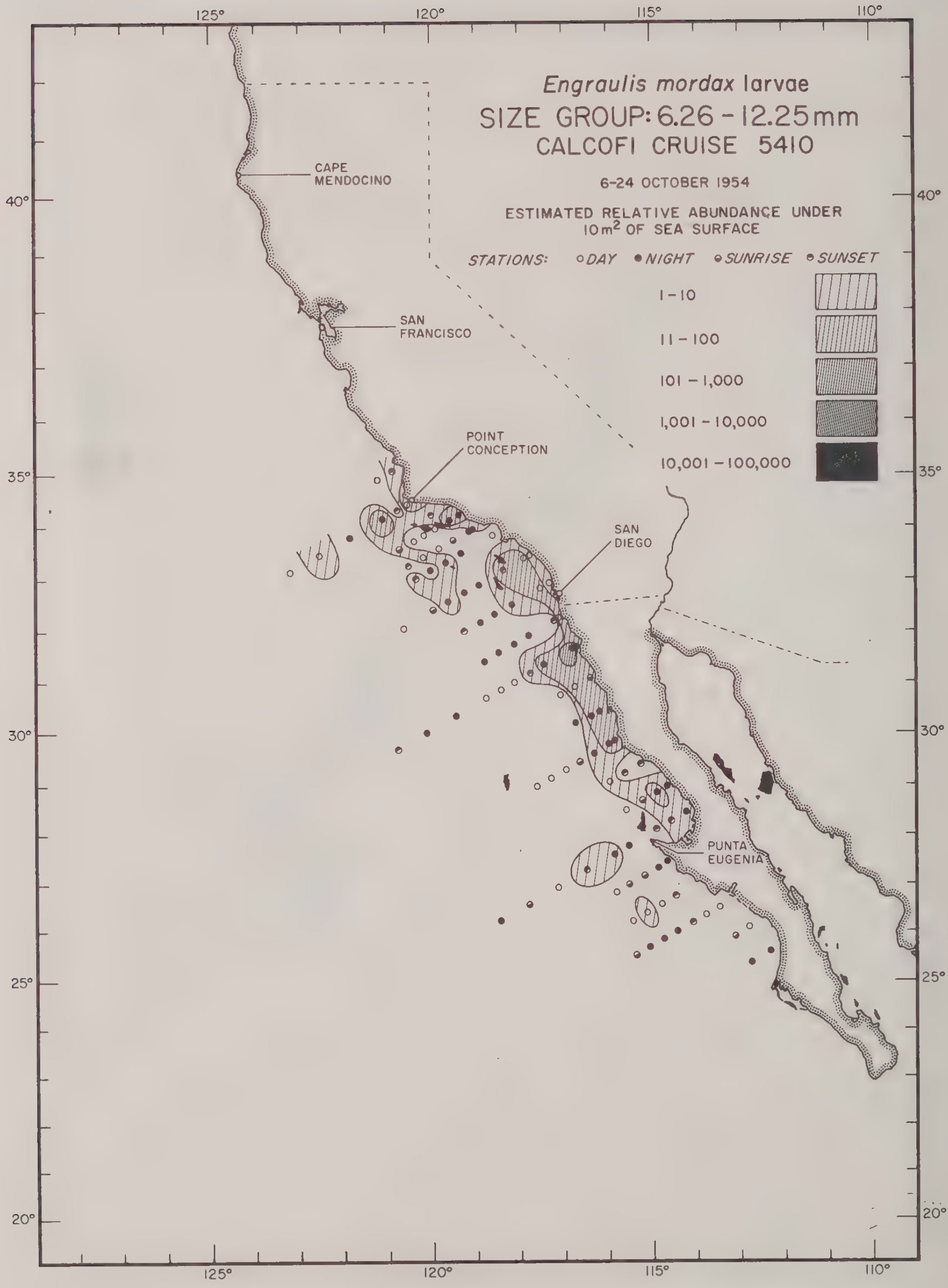
5408


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5408
18 AUGUST–10 SEPTEMBER 1954
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1–10
11–100
101–1,000
1,001–10,000
10,001–100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

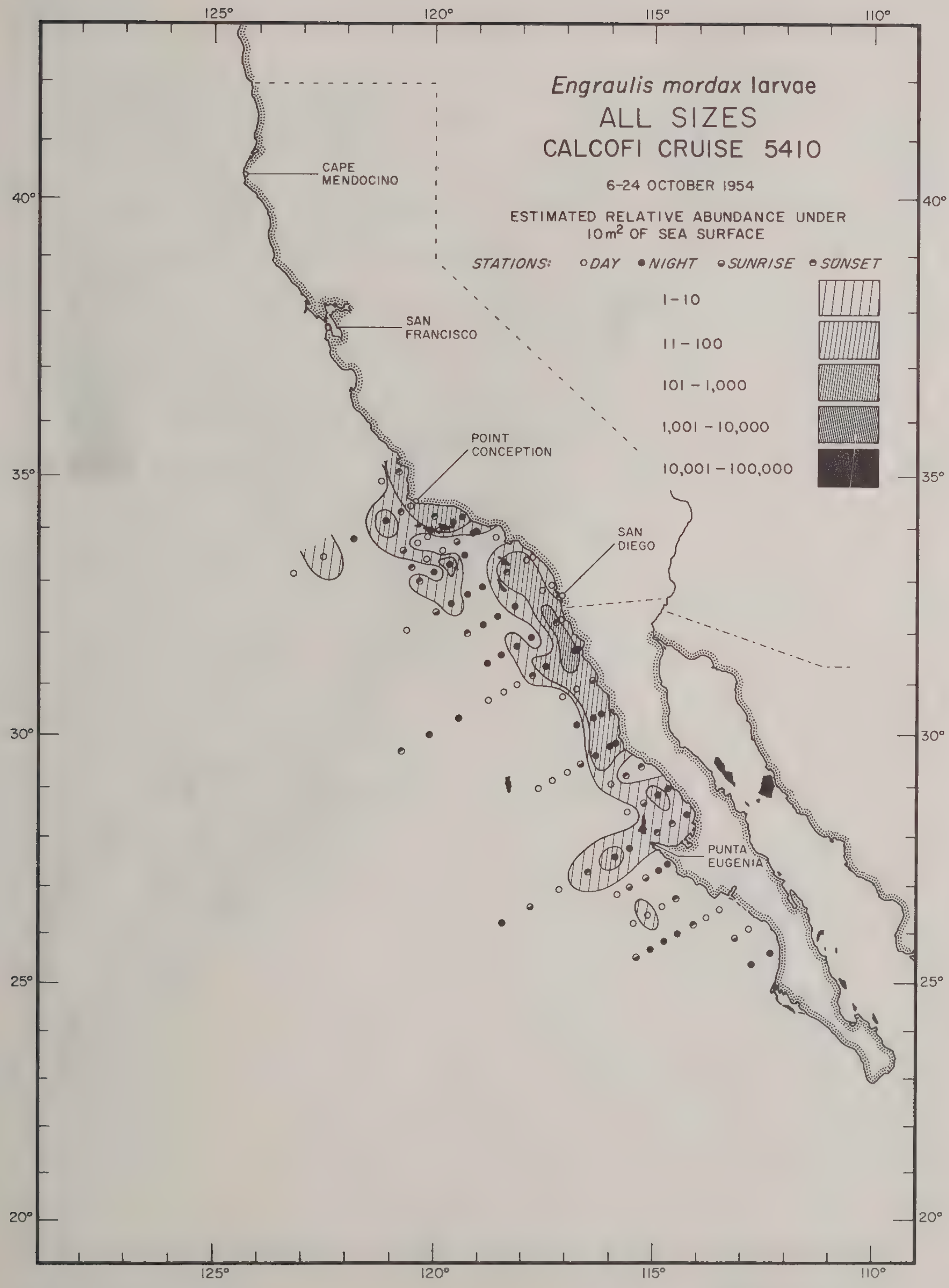
5408


125°
120°
115°
110°
Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5410
6-24 OCTOBER 1954
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ *DAY* ● *NIGHT* ◐ *SUNRISE* ◑ *SUNSET*
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
40°
35°
30°
25°
20°

Engraulis mordax larvae

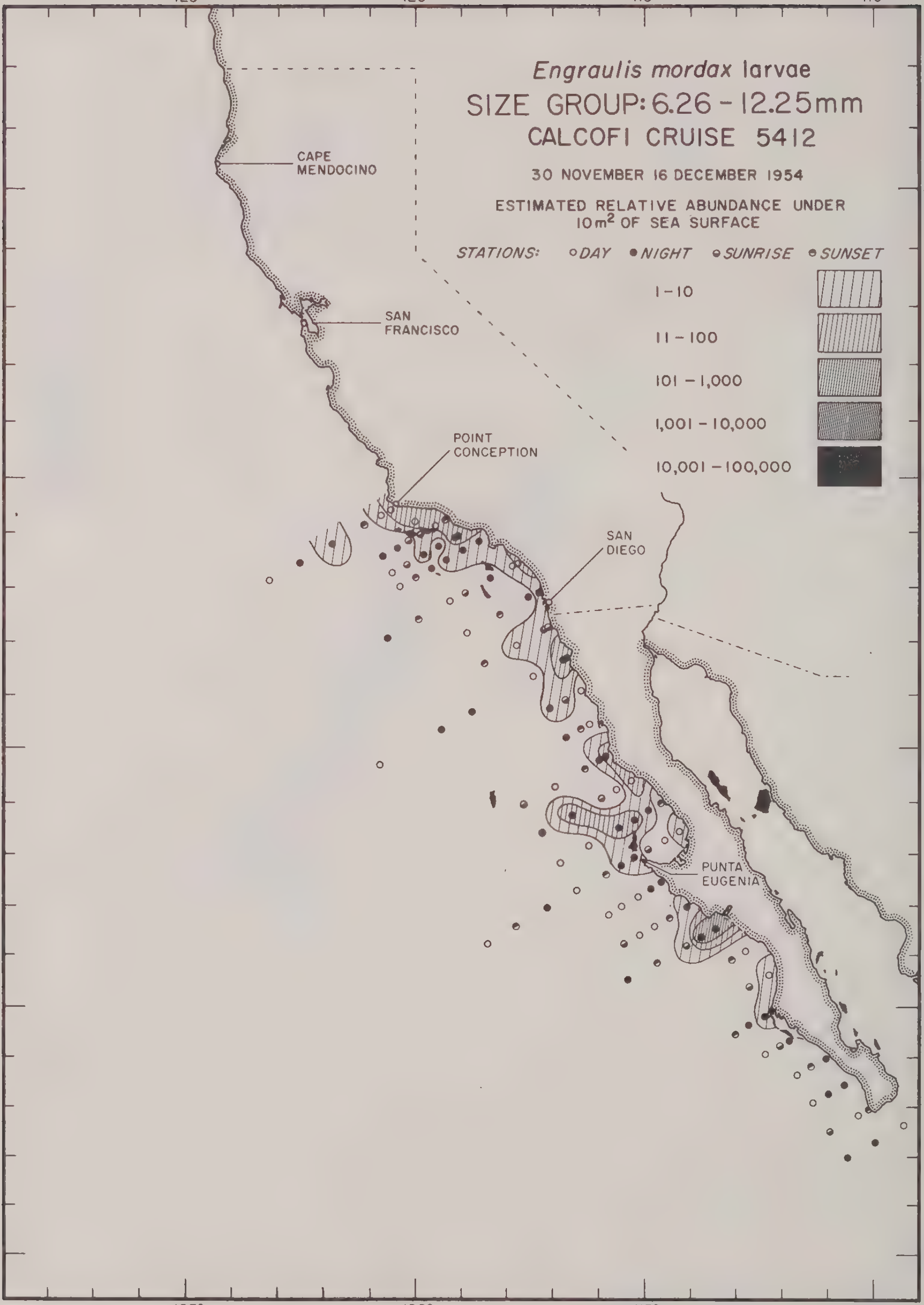
Size Group: 6.26-12.25mm

5410


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5410
6-24 OCTOBER 1954
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

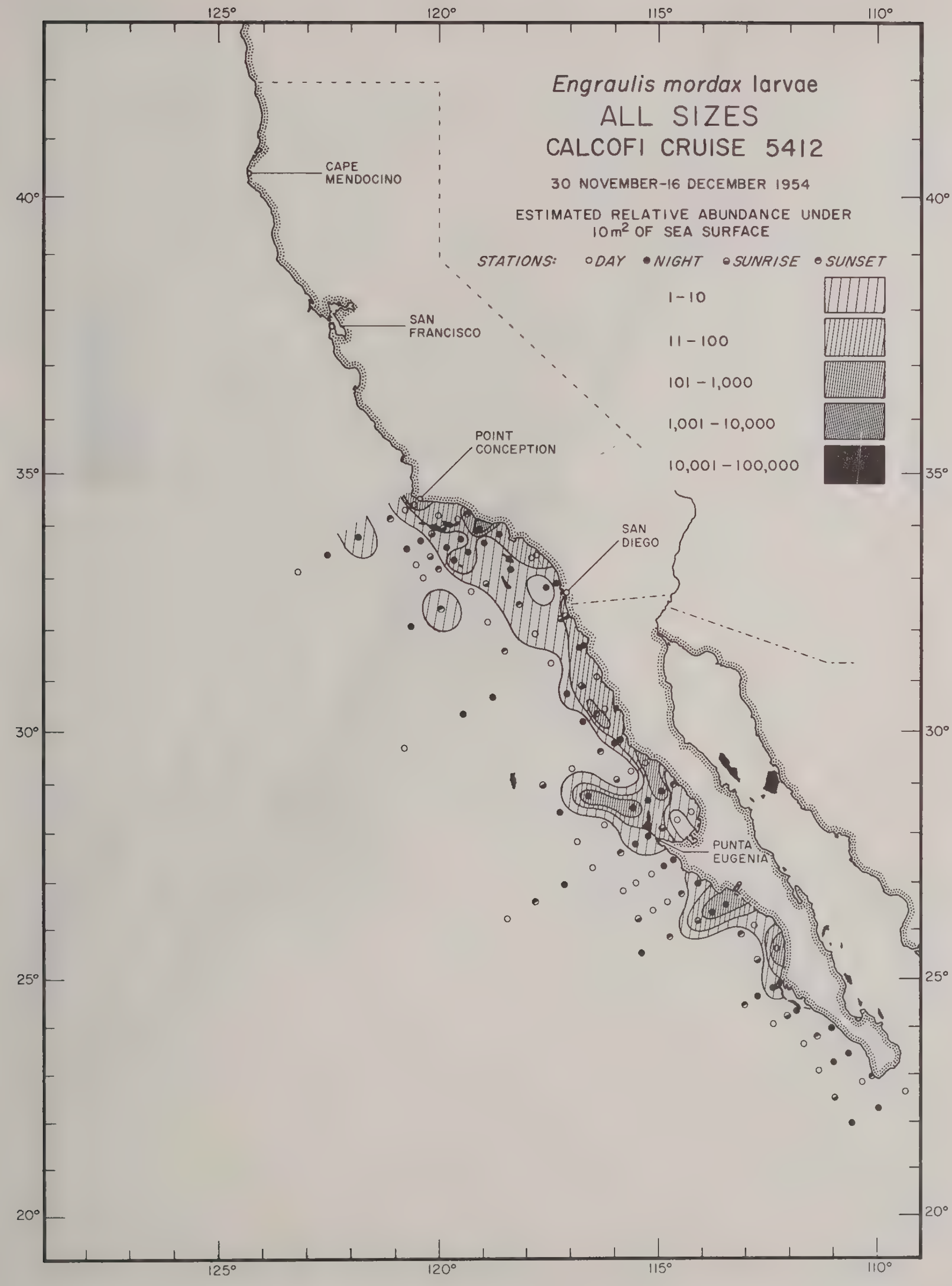
All Sizes
5410


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5412
30 NOVEMBER 16 DECEMBER 1954
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ *DAY* ● *NIGHT* *SUNRISE* *SUNSET*
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

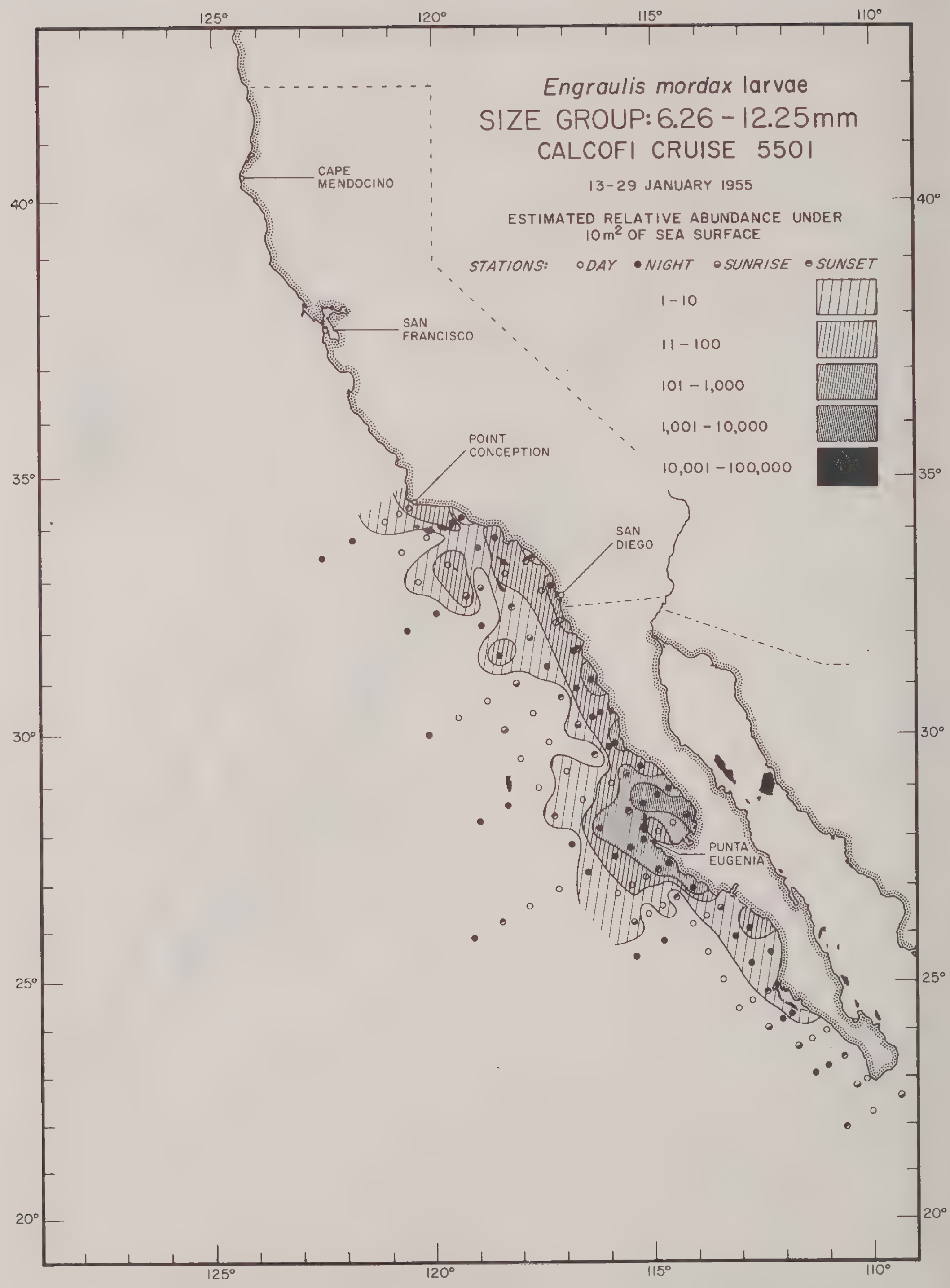
5412


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5412
30 NOVEMBER-16 DECEMBER 1954
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

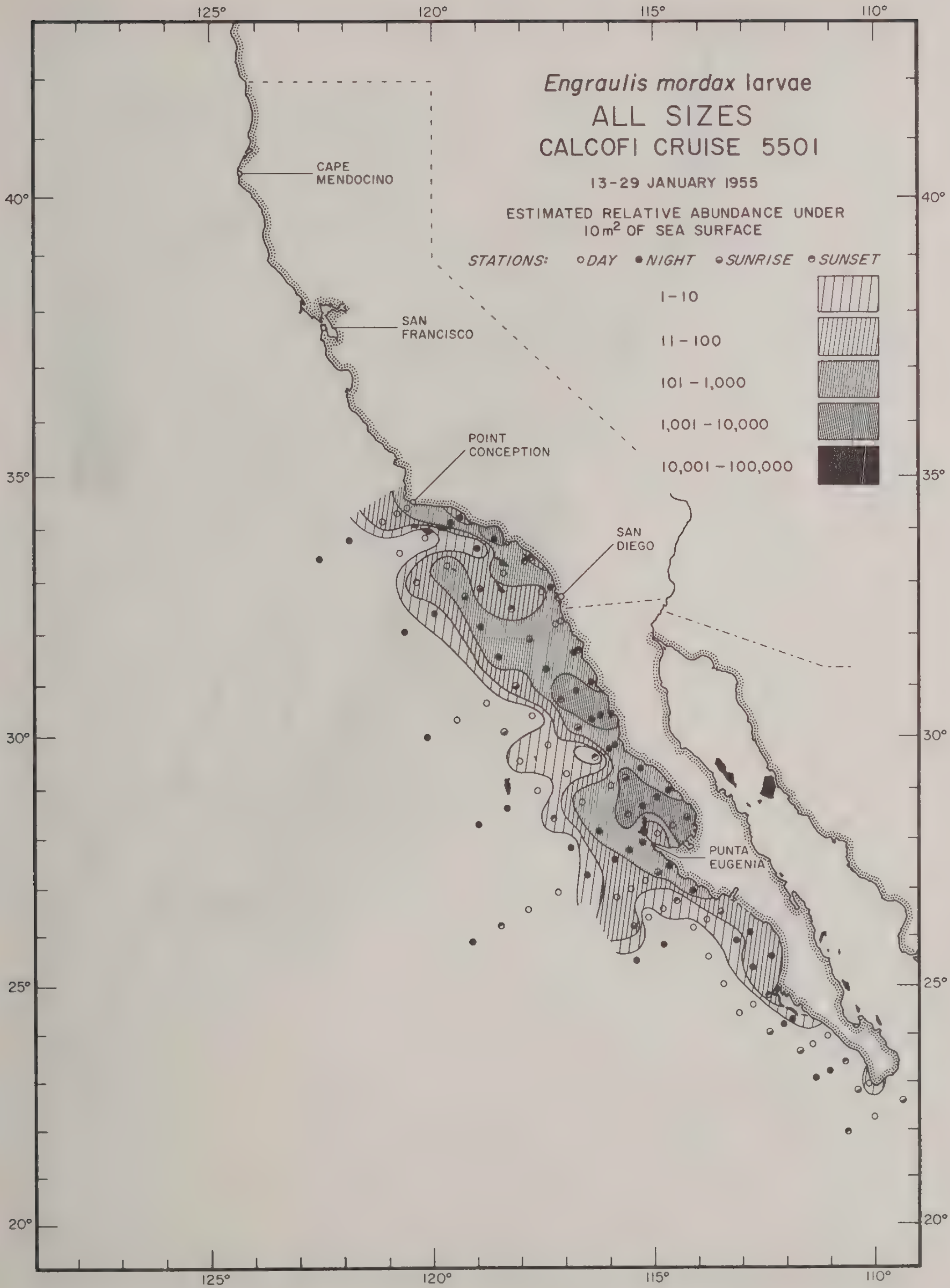
5412


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5501
13-29 JANUARY 1955
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

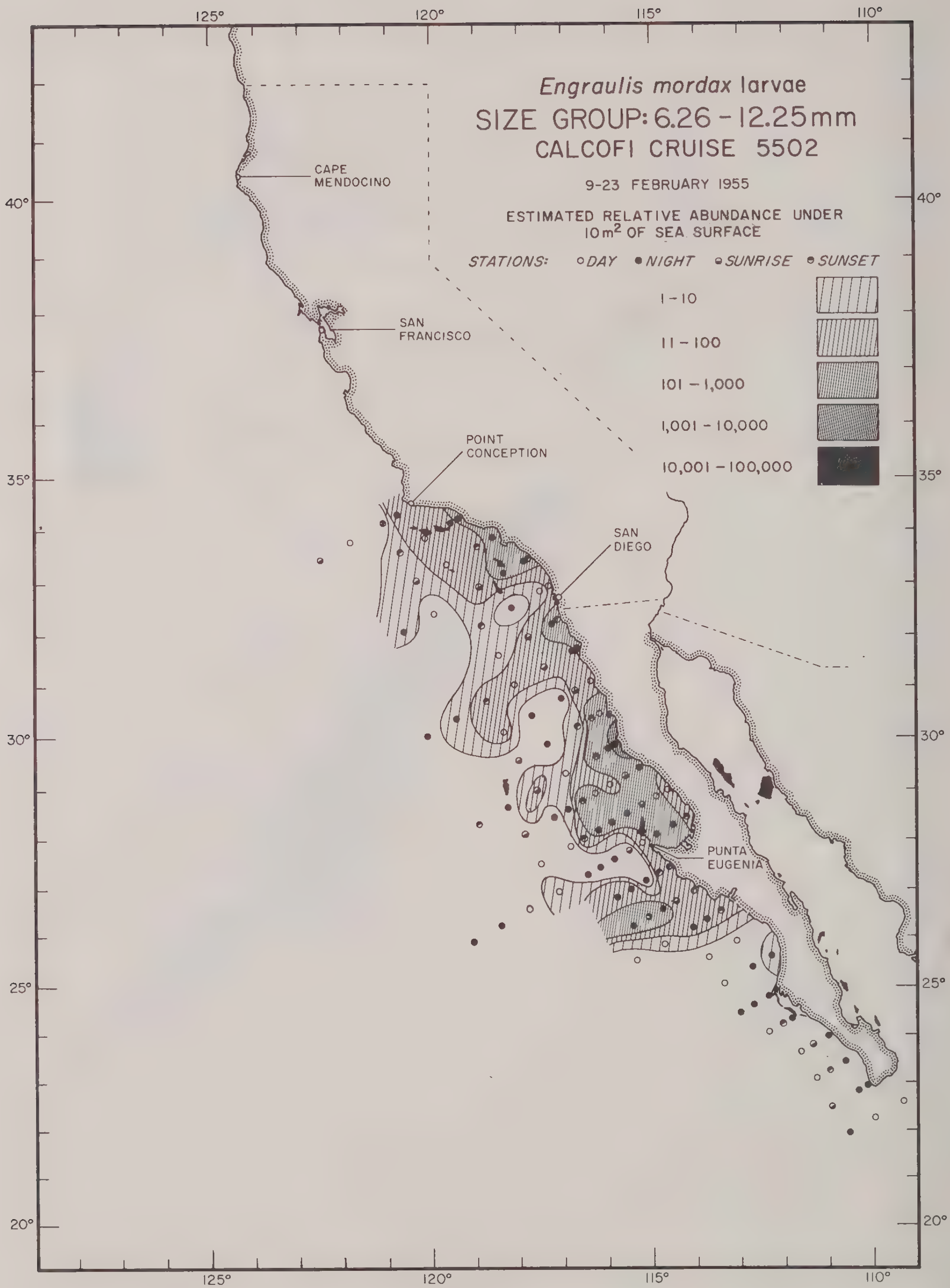
5501


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5501
13-29 JANUARY 1955
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○ *DAY* ● *NIGHT* ◒ *SUNRISE* ◓ *SUNSET*
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

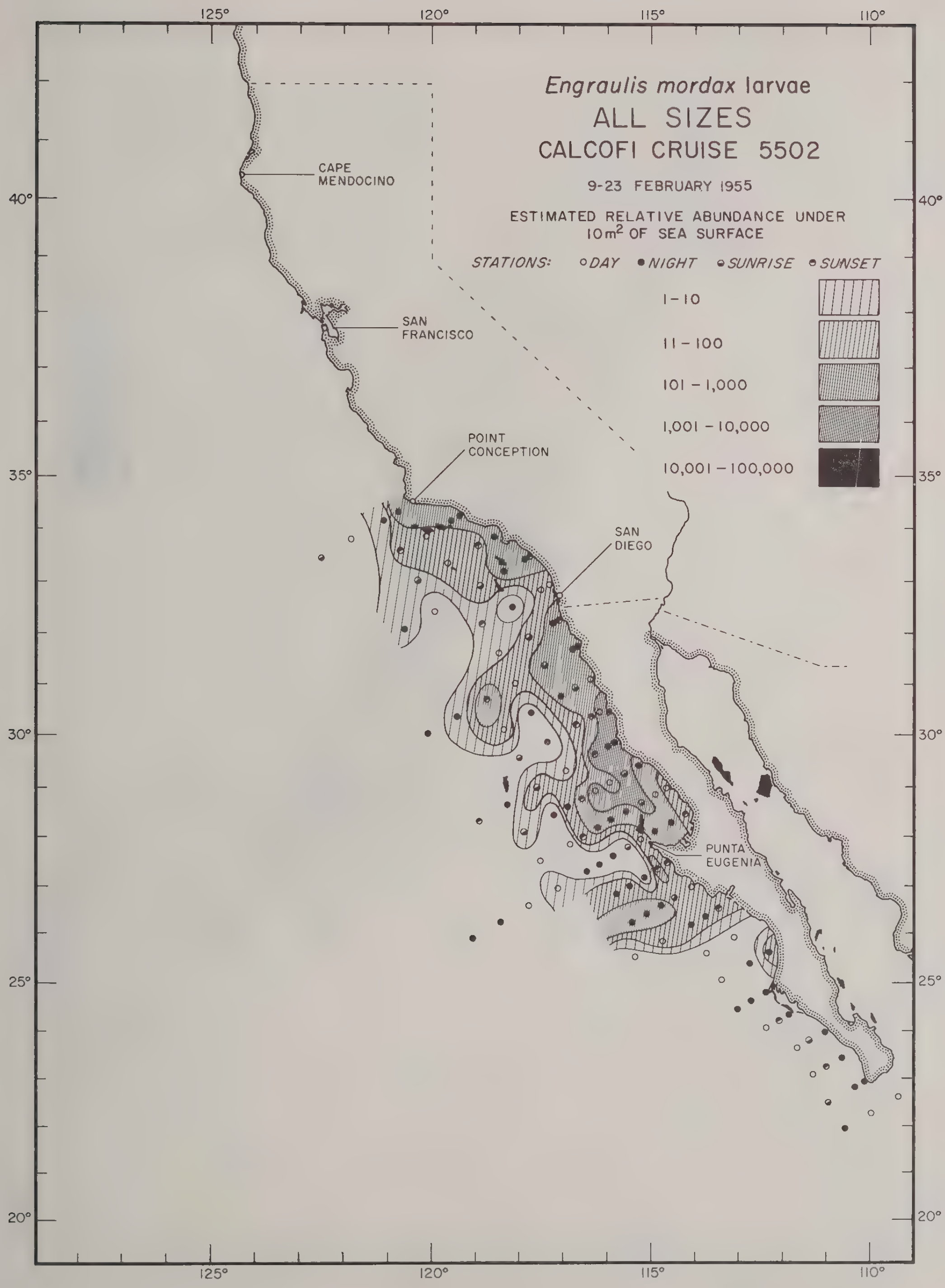
5501


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5502
9-23 FEBRUARY 1955
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

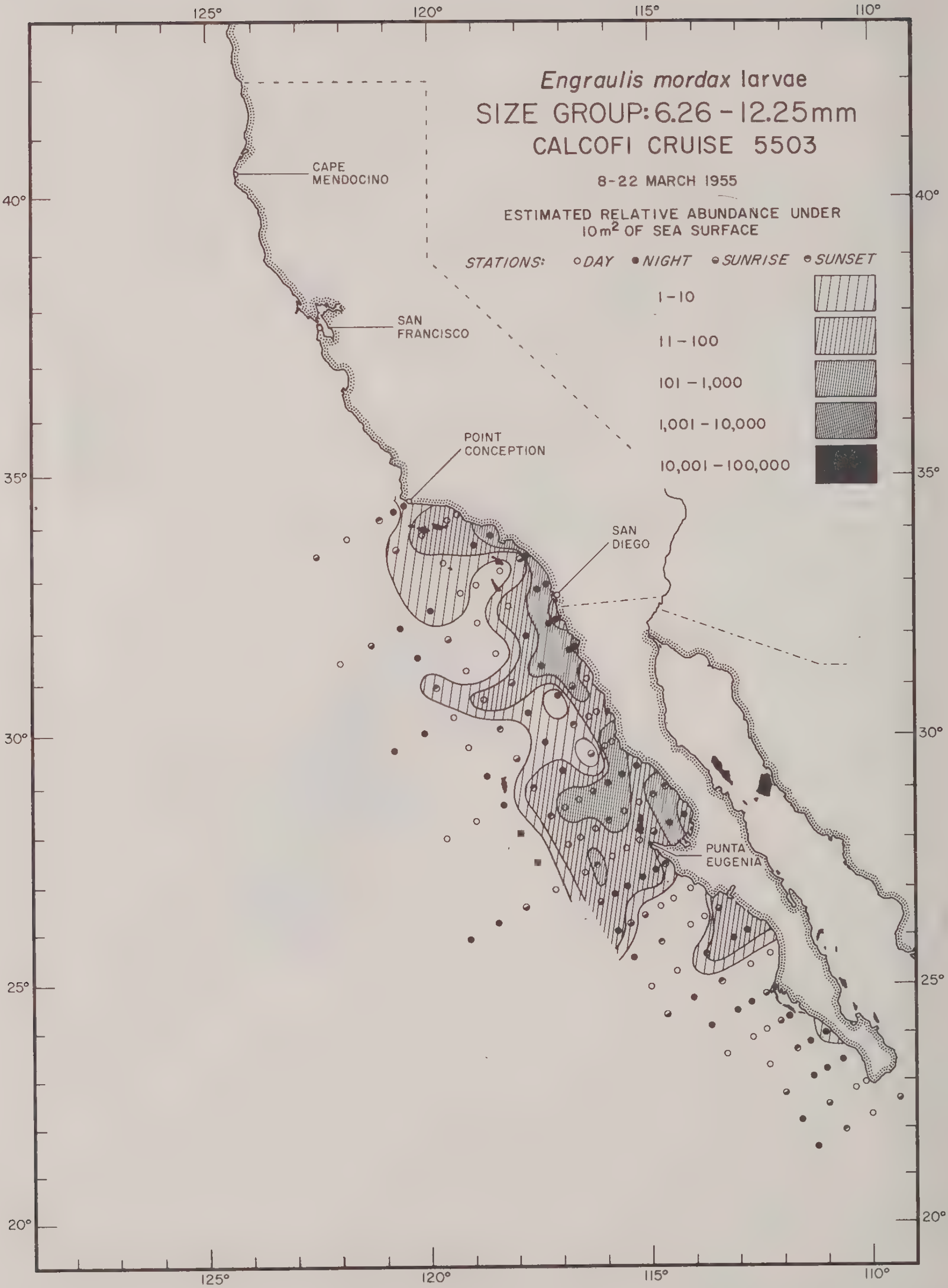
5502


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5502
9-23 FEBRUARY 1955
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

All Sizes

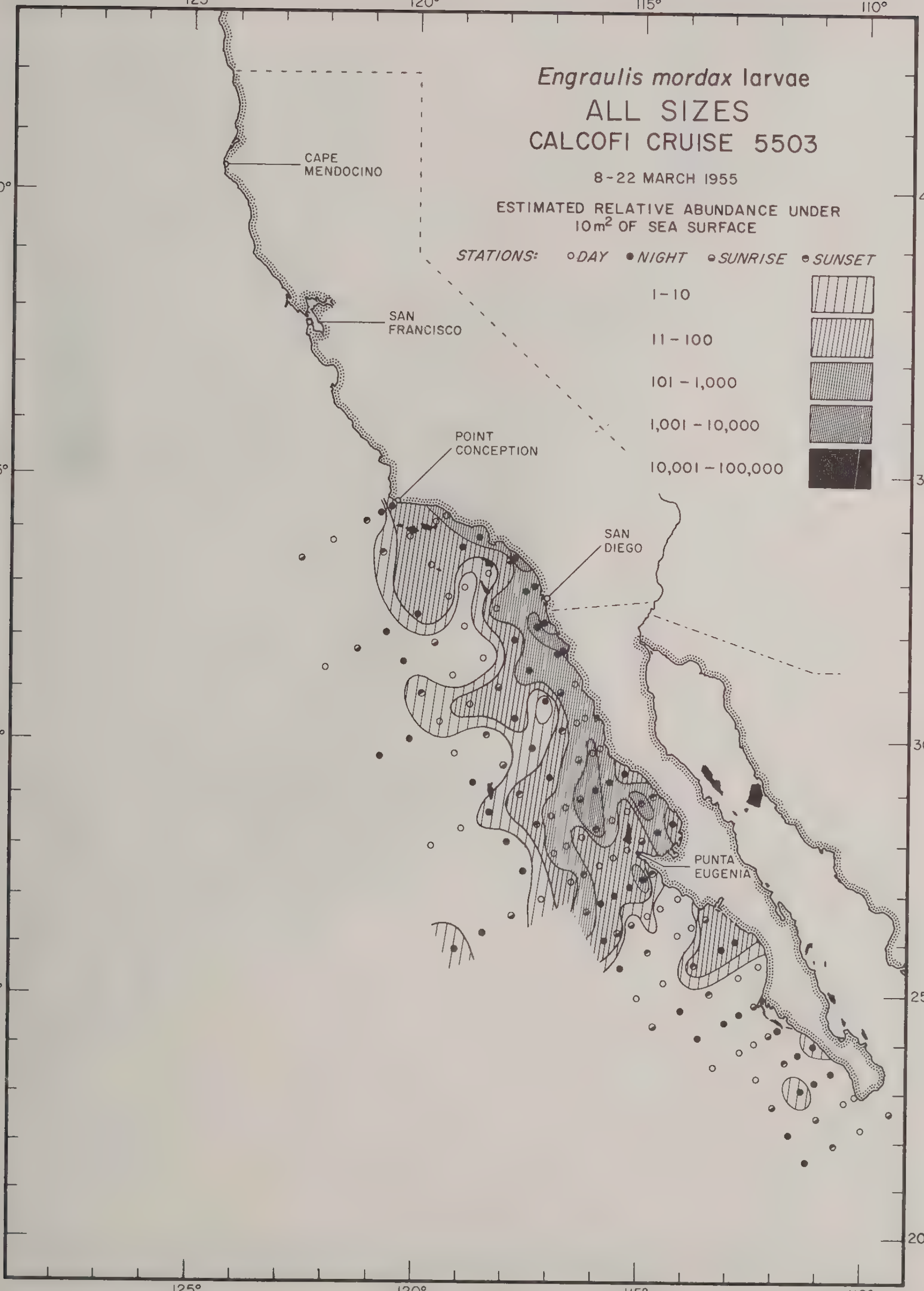
5502


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5503
8-22 MARCH 1955
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

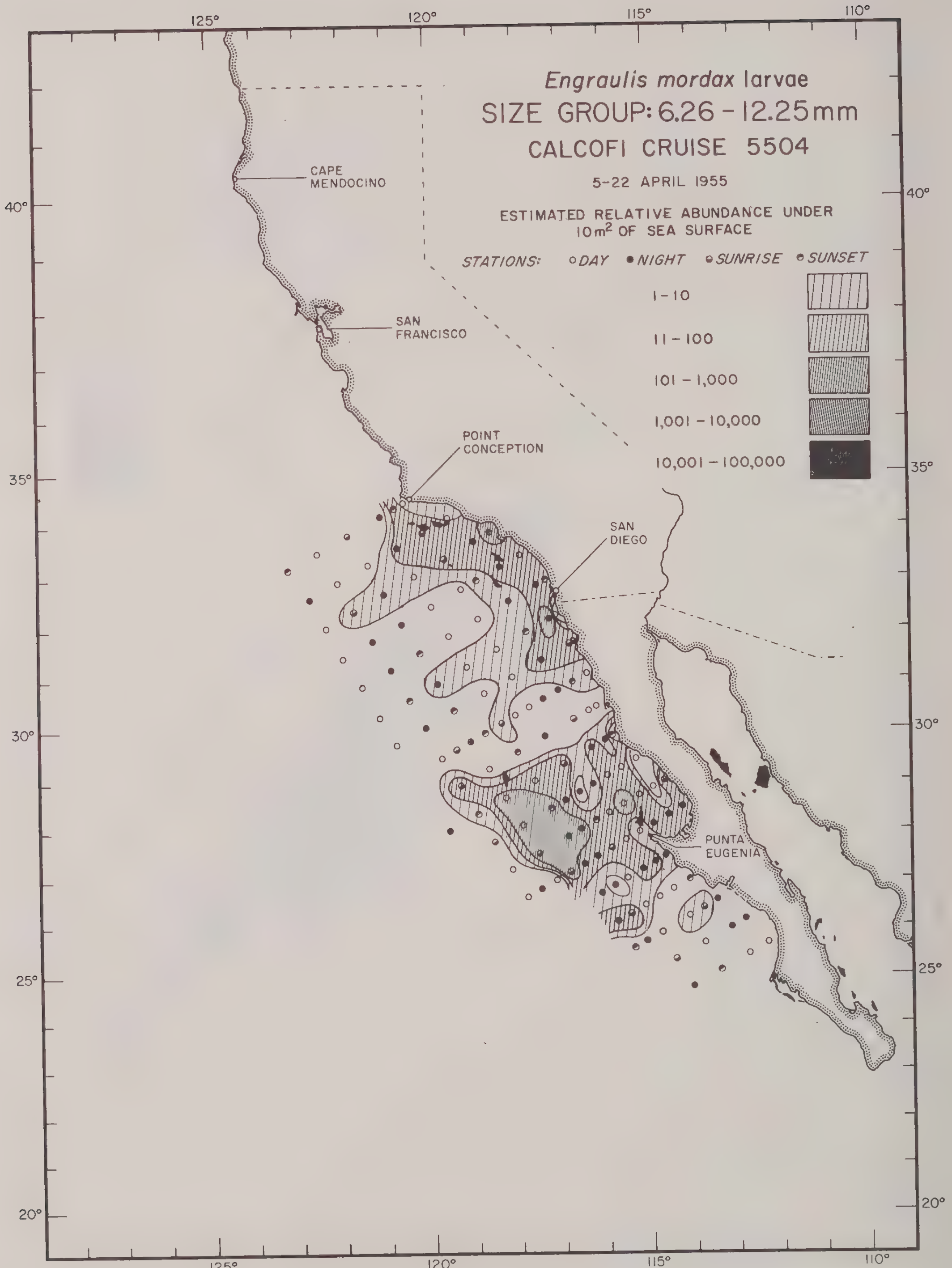
5503


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5503
8-22 MARCH 1955
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

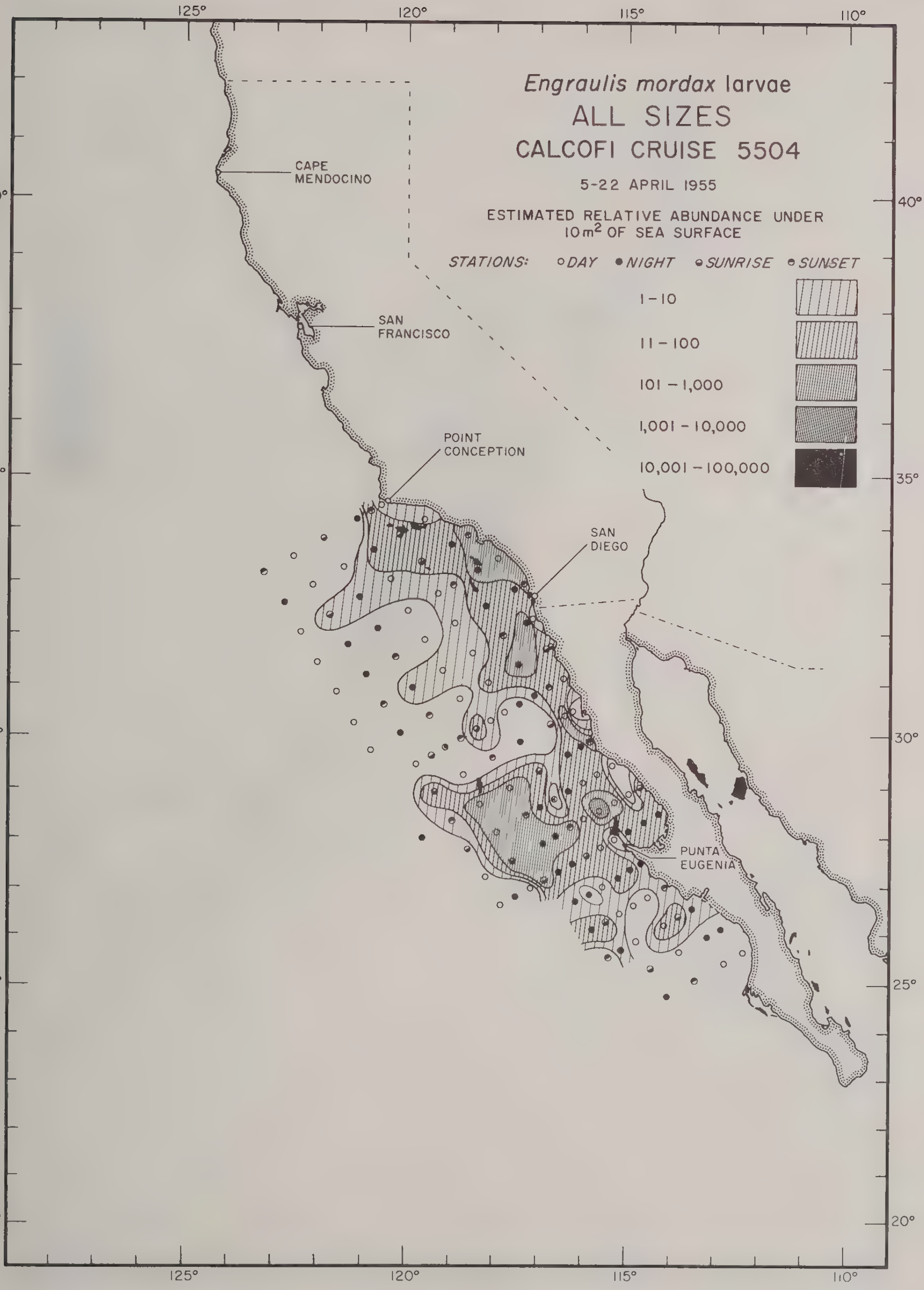
5503


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5504
5-22 APRIL 1955
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

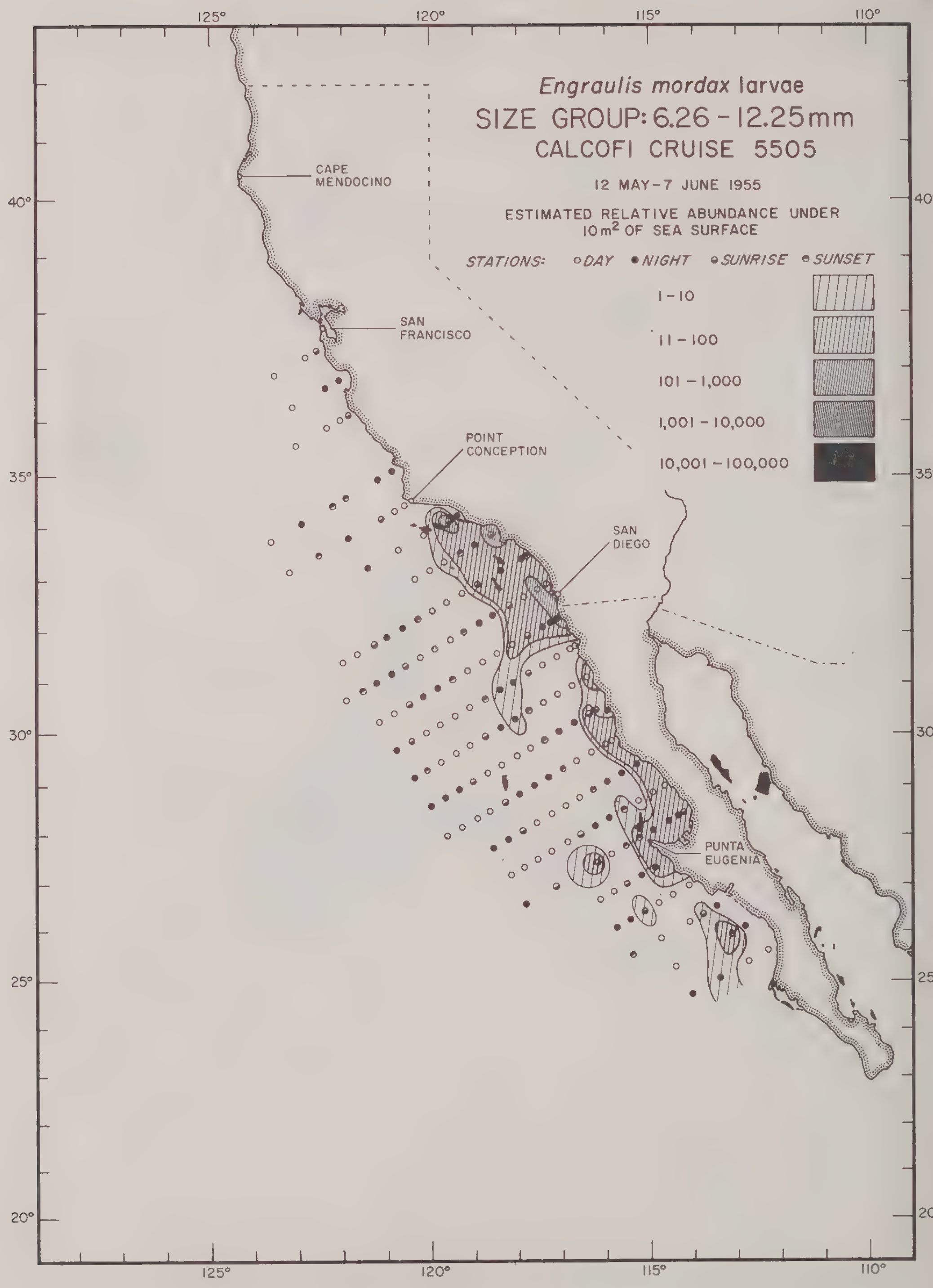
5504


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5504
5-22 APRIL 1955
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

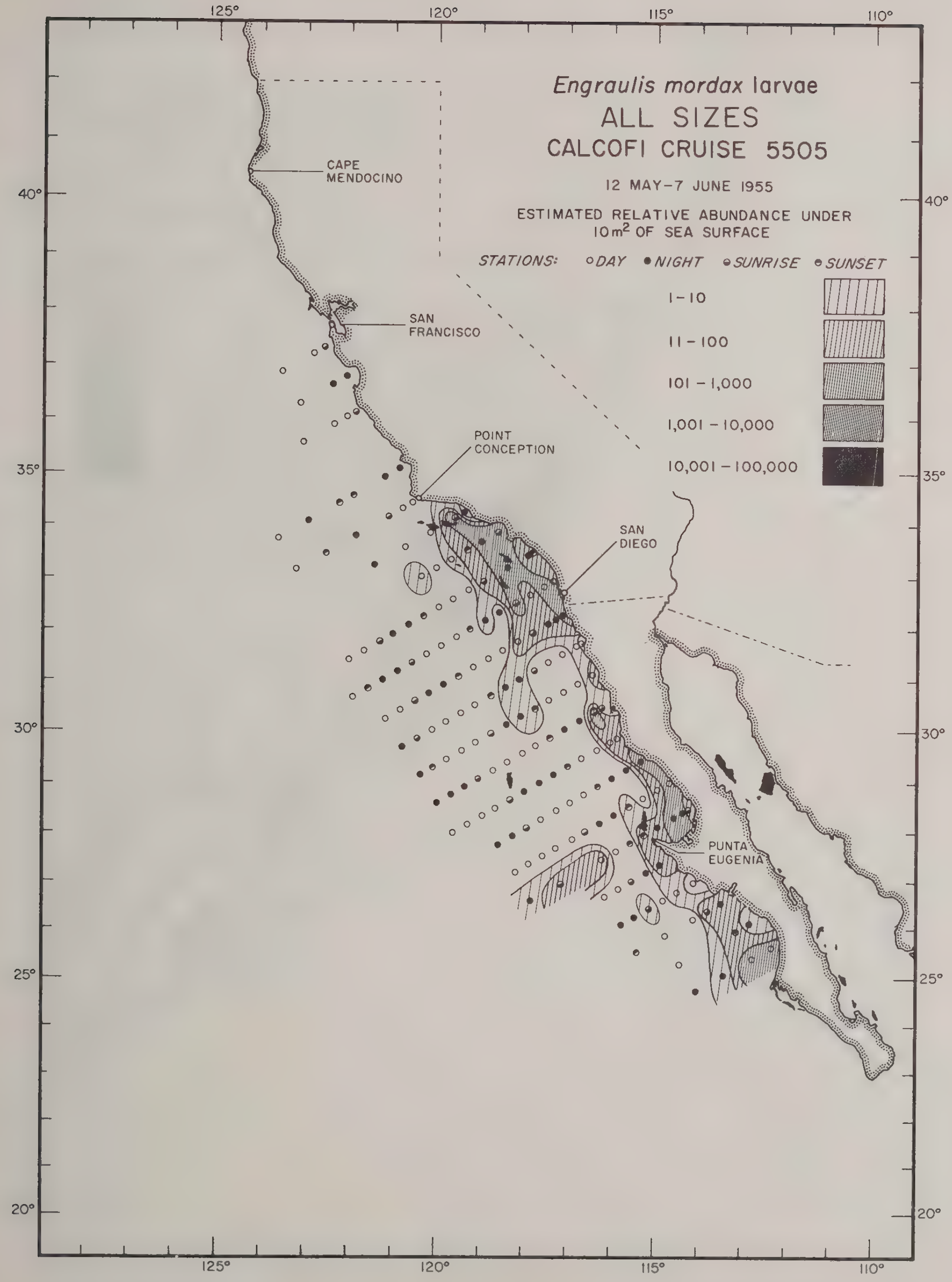
5504


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5505
12 MAY-7 JUNE 1955
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

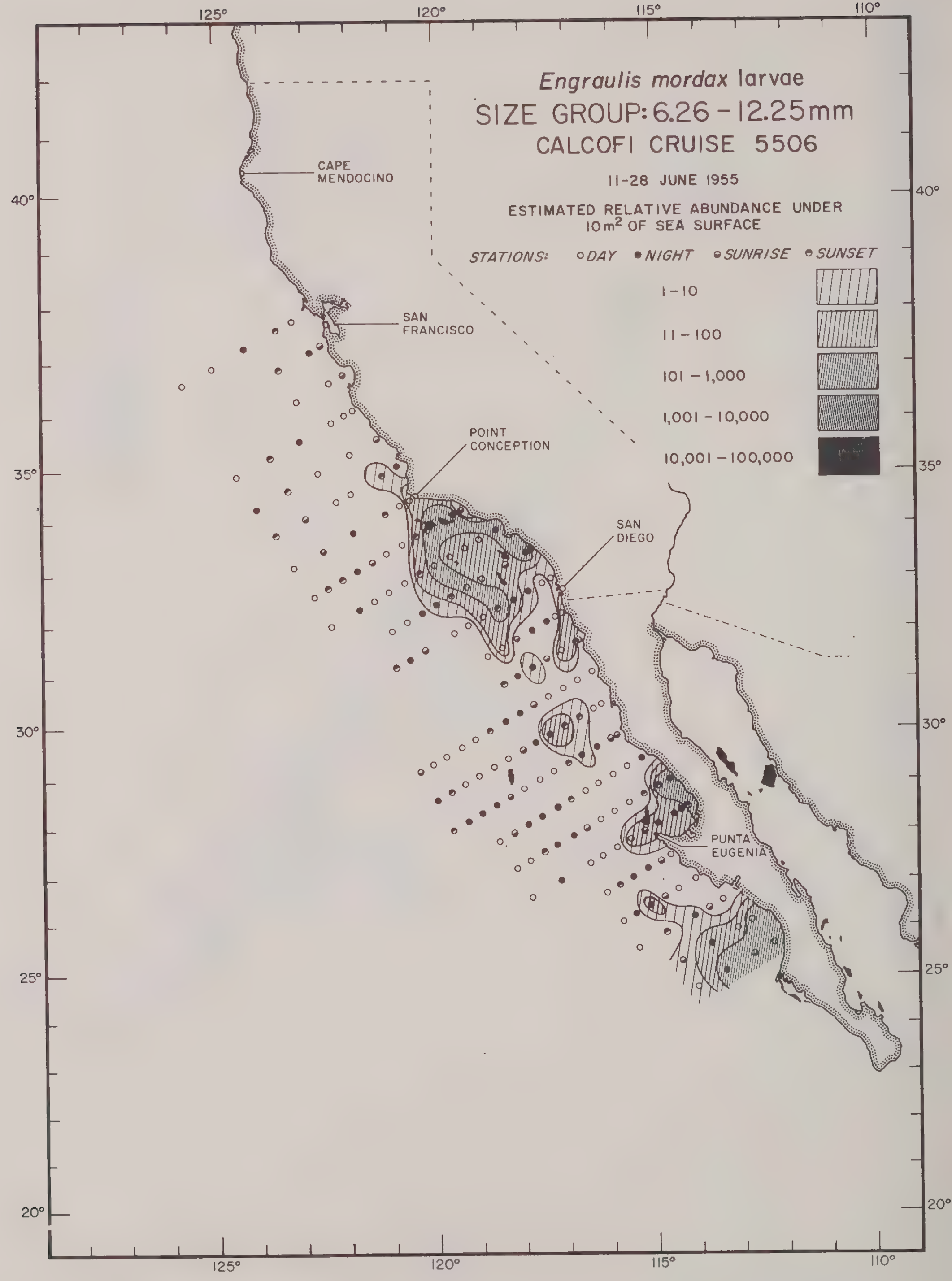
5505


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5505
12 MAY–7 JUNE 1955
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◐SUNRISE ◑SUNSET
1–10
11–100
101–1,000
1,001–10,000
10,001–100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

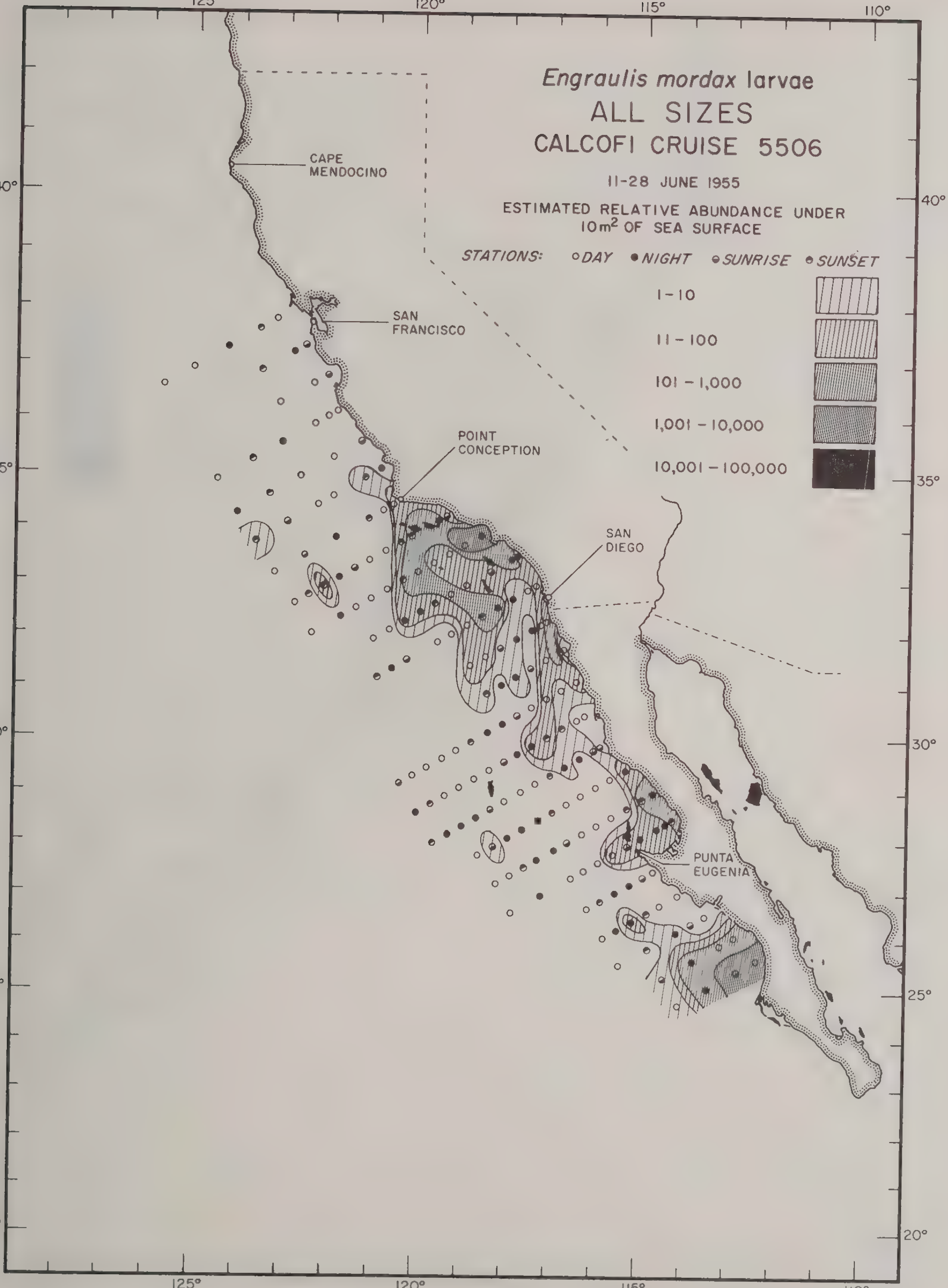
5505


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5506
11-28 JUNE 1955
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

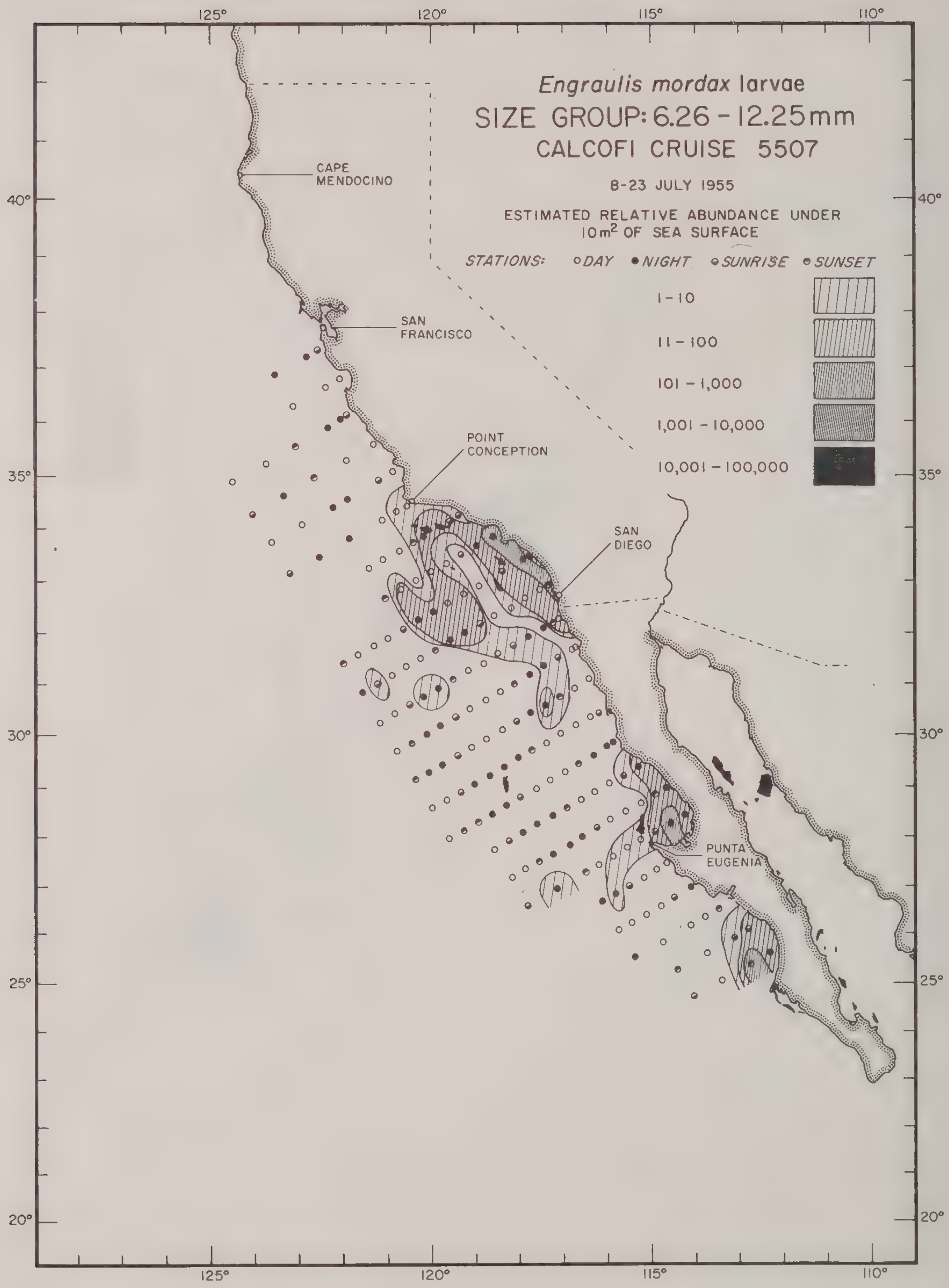
5506


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5506
11-28 JUNE 1955
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◐SUNRISE ◑SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

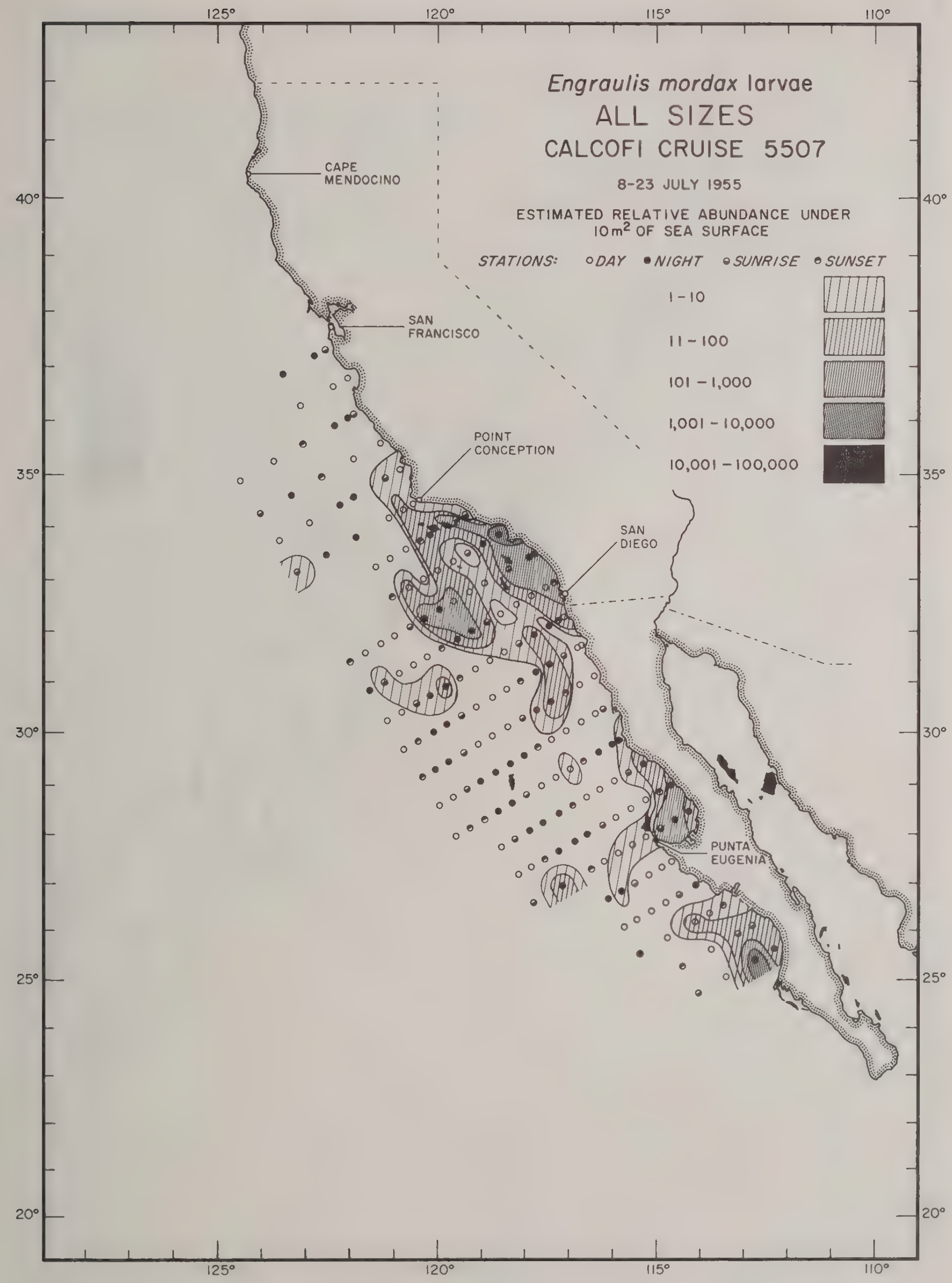
5506


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5507
8-23 JULY 1955
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

Size Group: 6.26-12.25mm

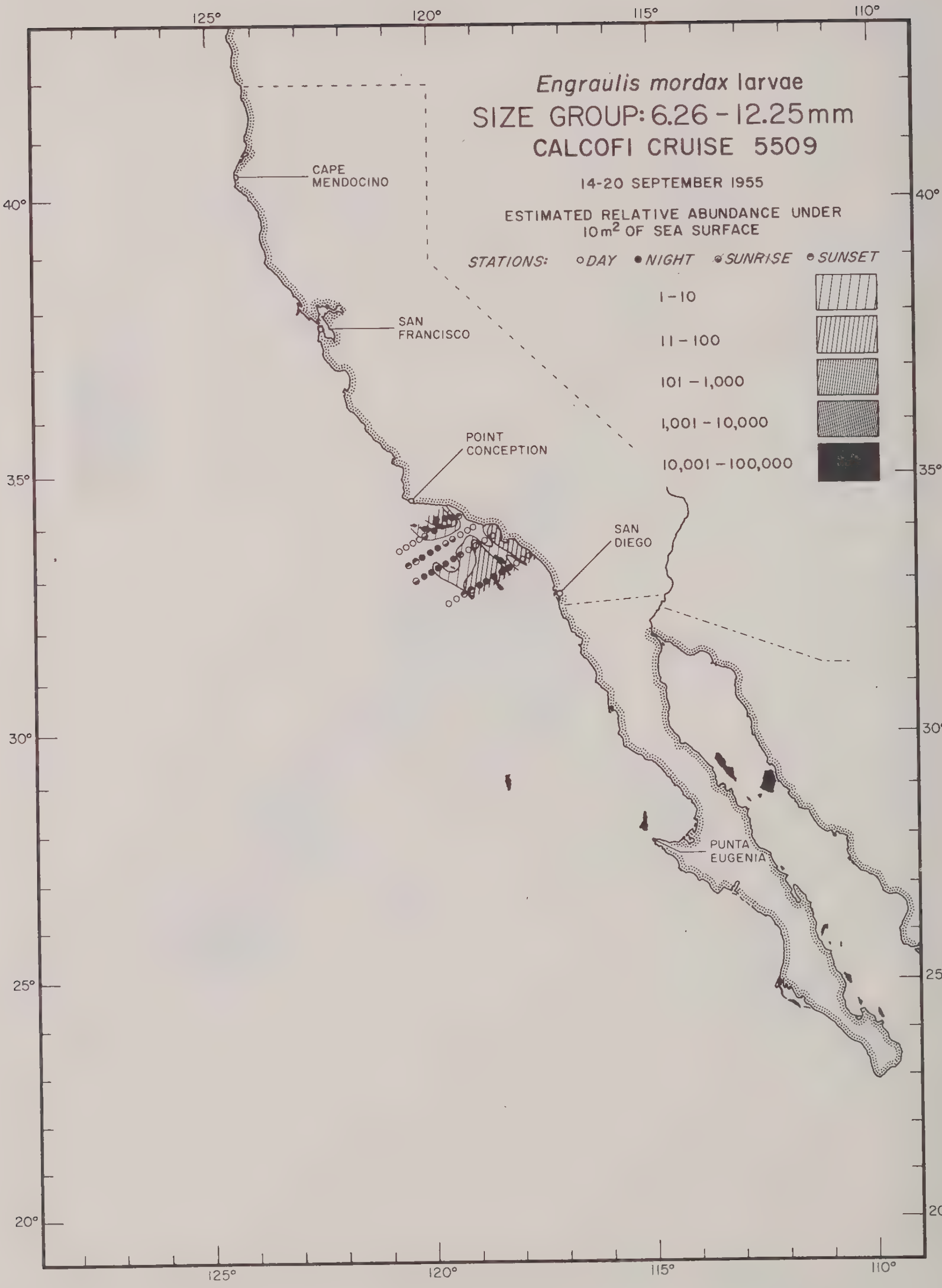
5507


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5507
8-23 JULY 1955
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

5507

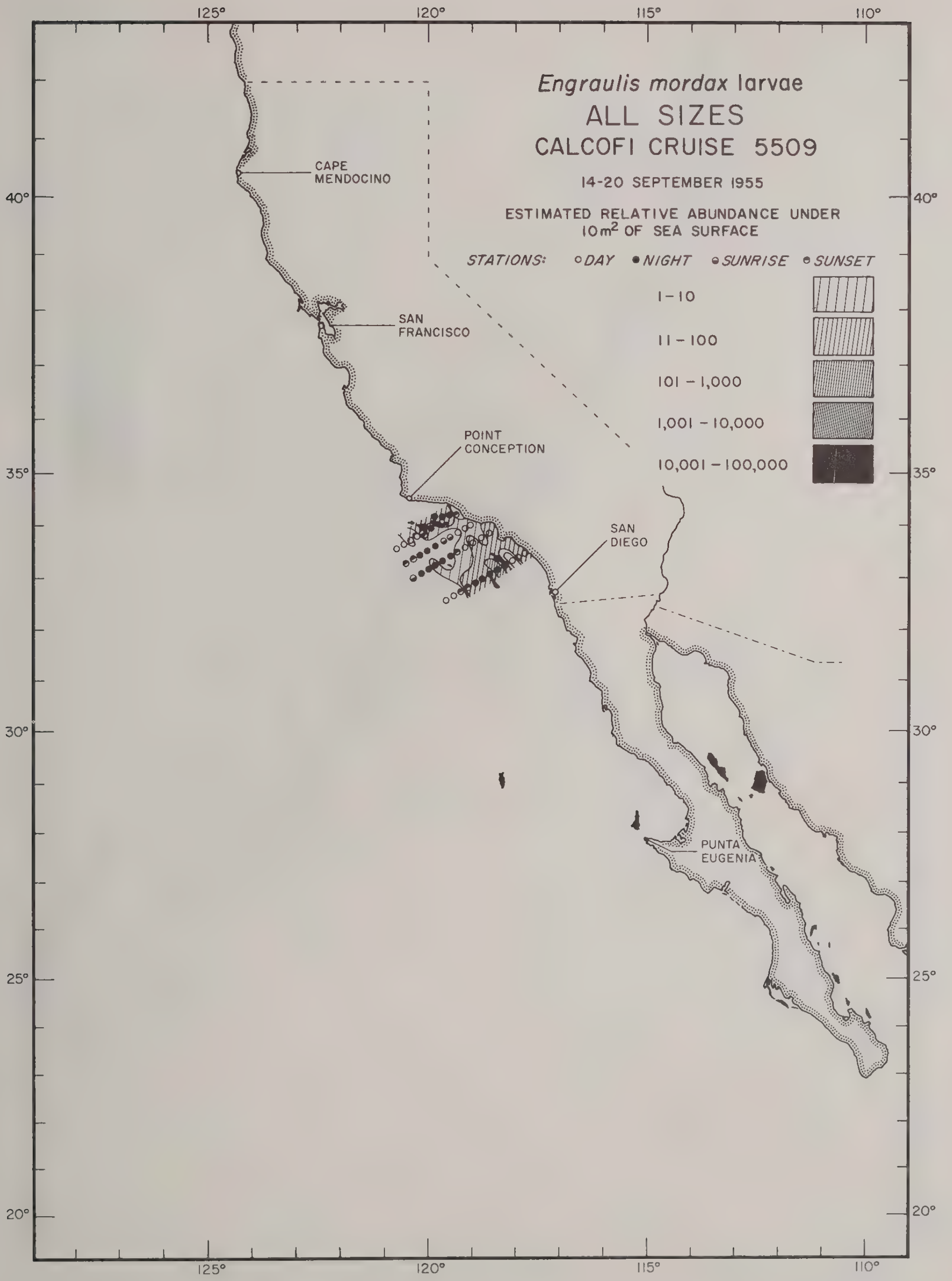


125°
120°
115°
110°
Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5509
14-20 SEPTEMBER 1955
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ *DAY* ● *NIGHT* *SUNRISE* *SUNSET*
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
40°
35°
30°
25°
20°

Engraulis mordax larvae

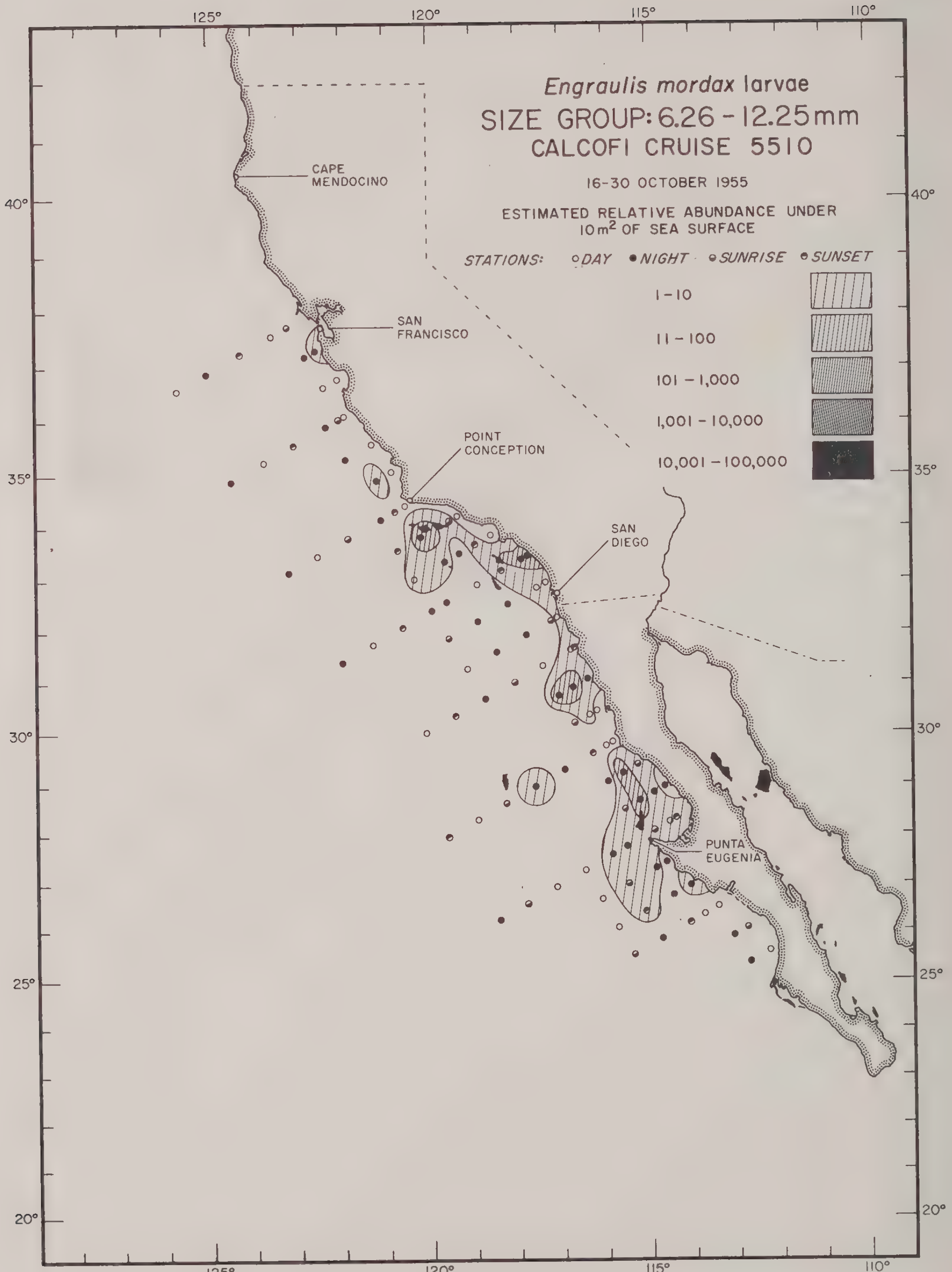
Size Group: 6.26-12.25mm

5509


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5509
14-20 SEPTEMBER 1955
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

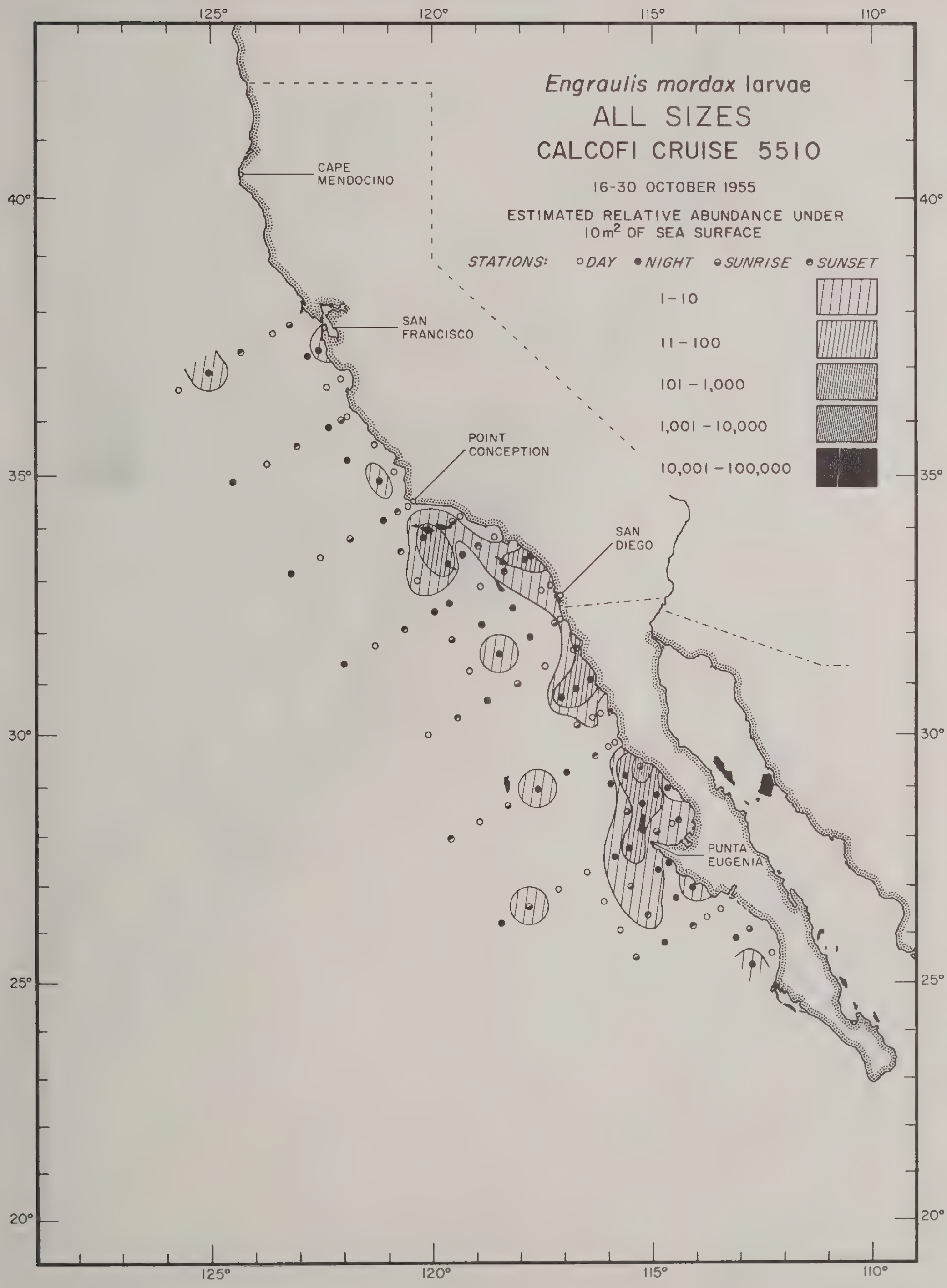
All Sizes
5509


125°
120°
115°
110°
Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5510
16-30 OCTOBER 1955
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

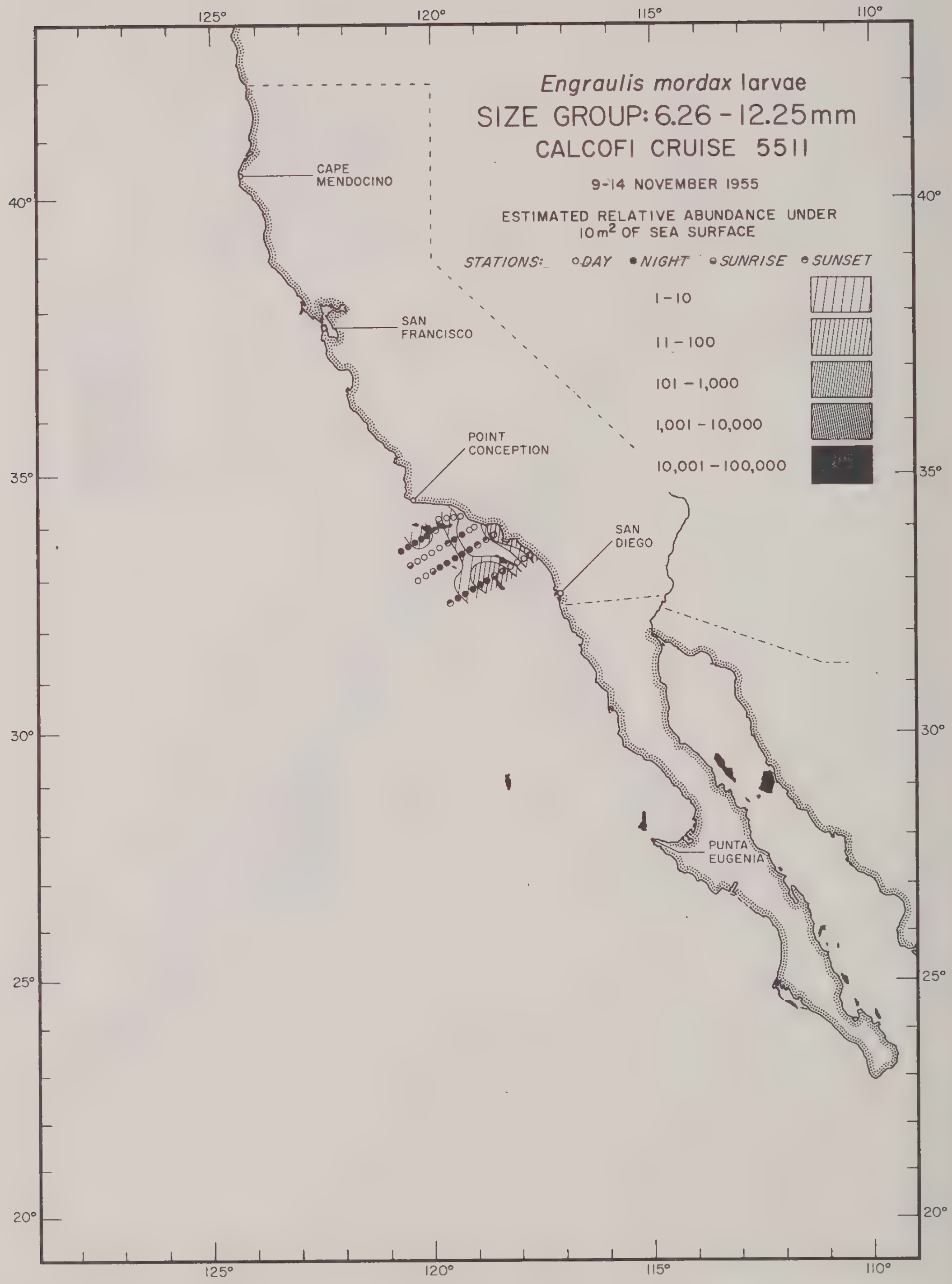
5510


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5510
16-30 OCTOBER 1955
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT SUNRISE SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

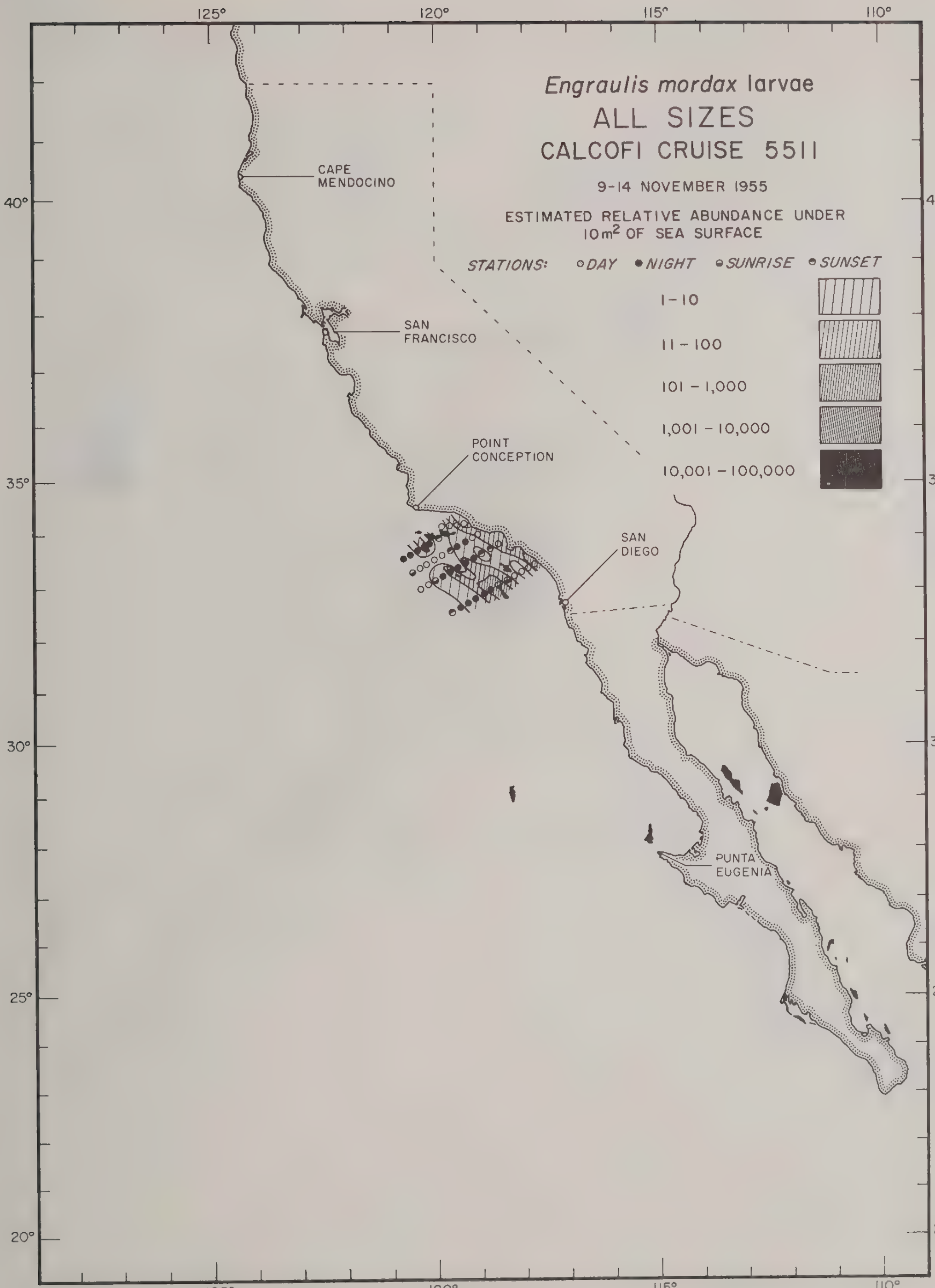
5510


125°
120°
115°
110°
Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5511
9-14 NOVEMBER 1955
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ *DAY* ● *NIGHT* ◐ *SUNRISE* ◑ *SUNSET*
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25 mm

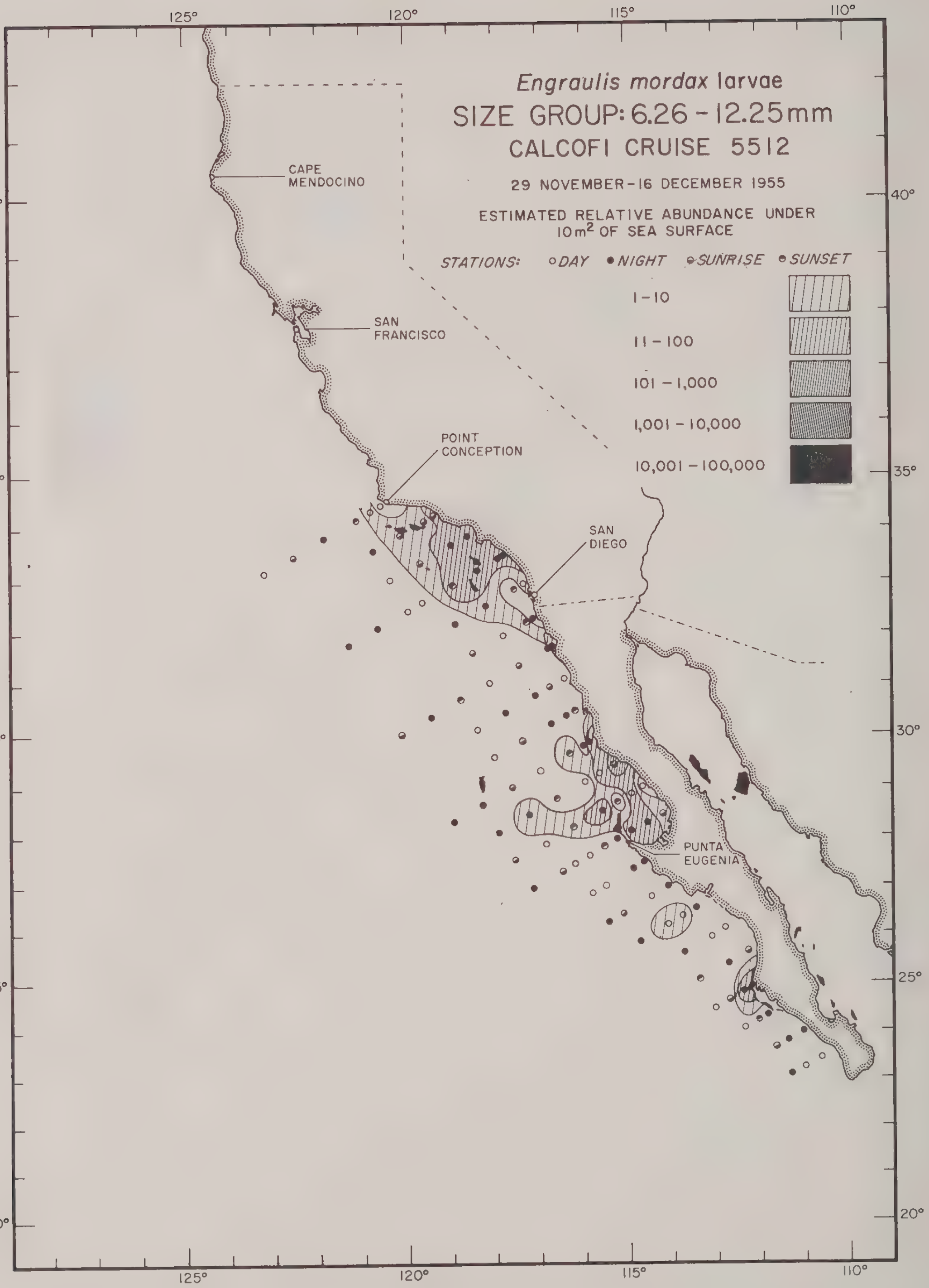
5511


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5511
9-14 NOVEMBER 1955
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

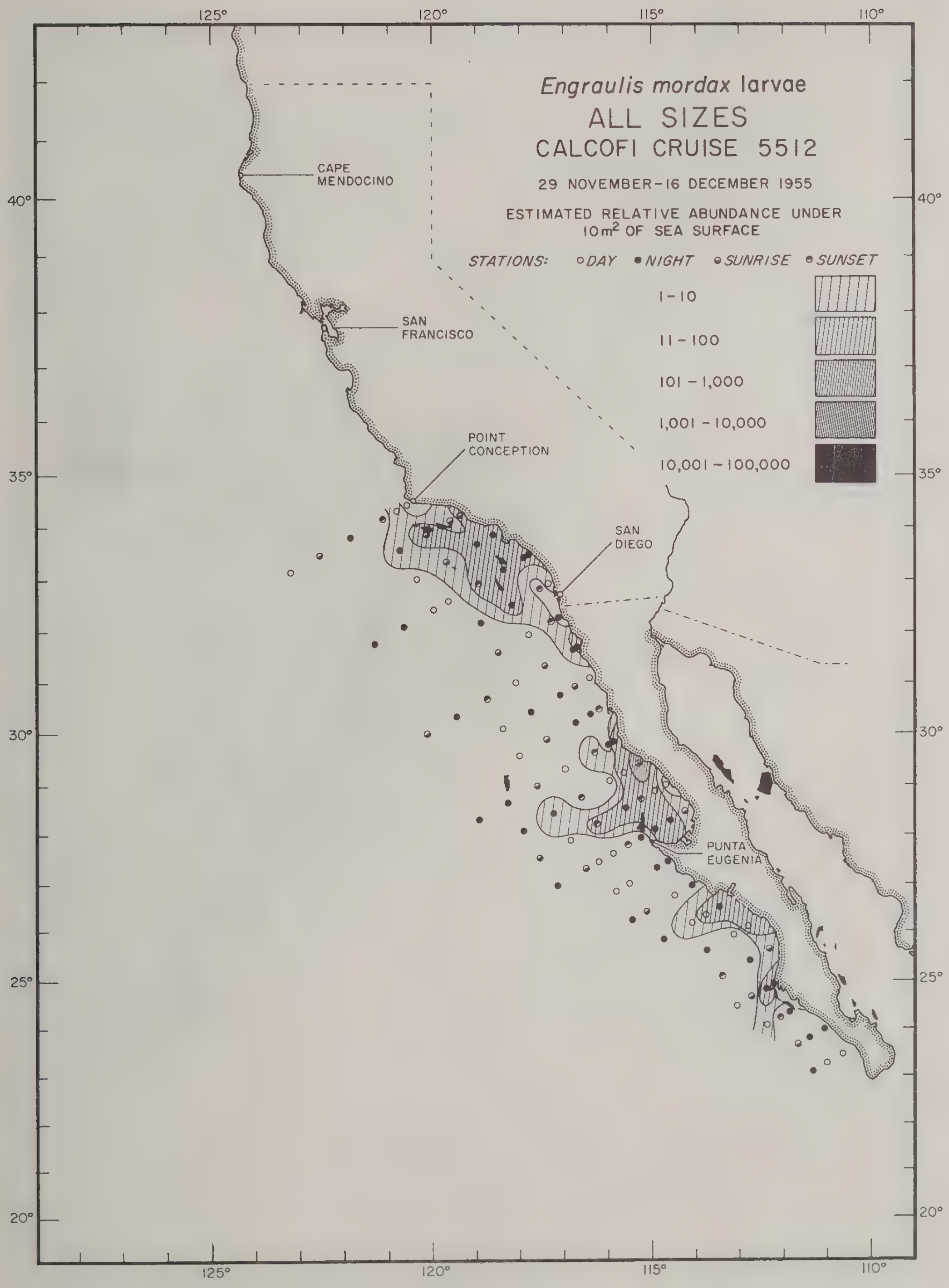
5511


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5512
29 NOVEMBER-16 DECEMBER 1955
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◐SUNRISE ◑SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

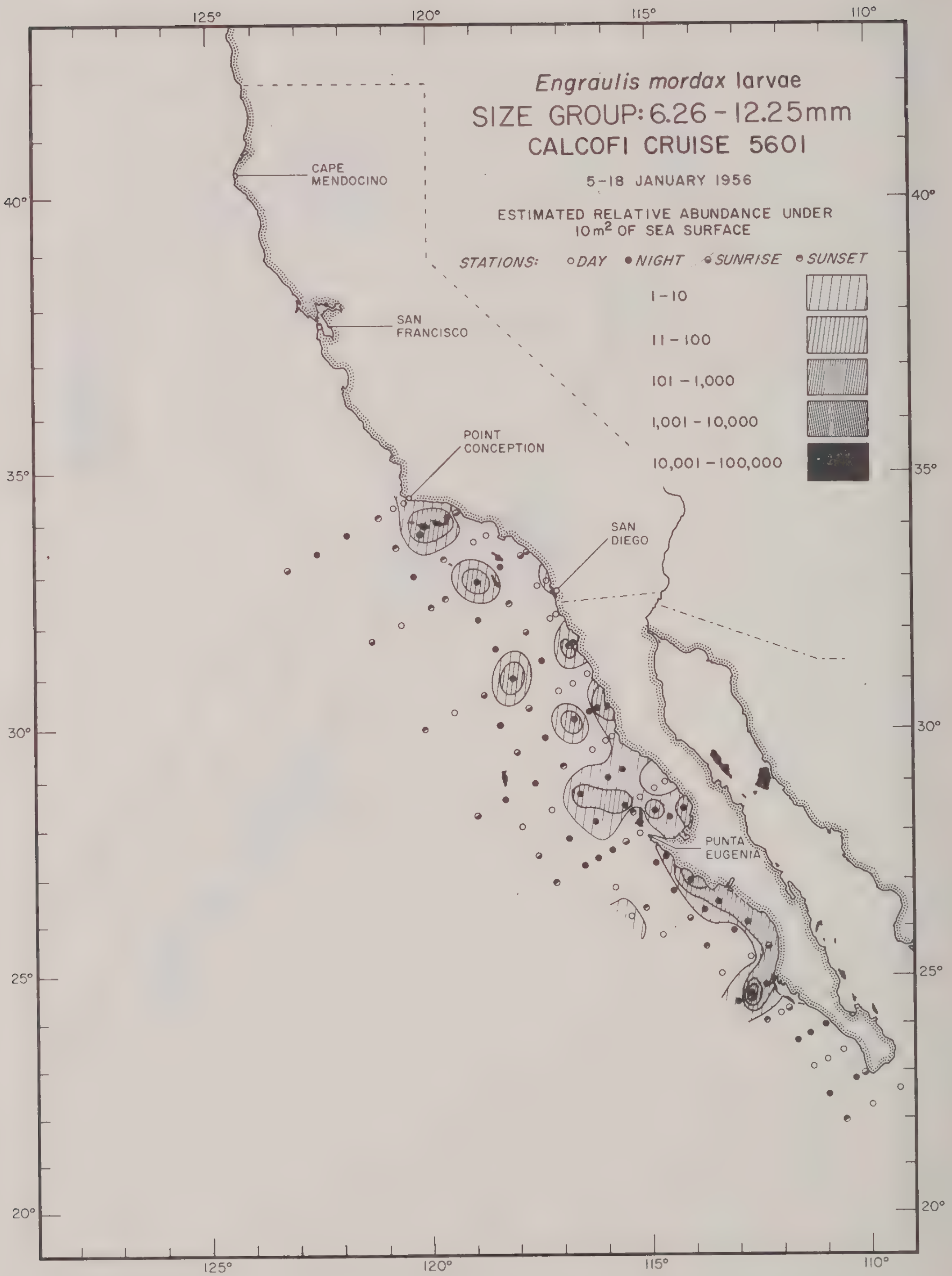
5512


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5512
29 NOVEMBER–16 DECEMBER 1955
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

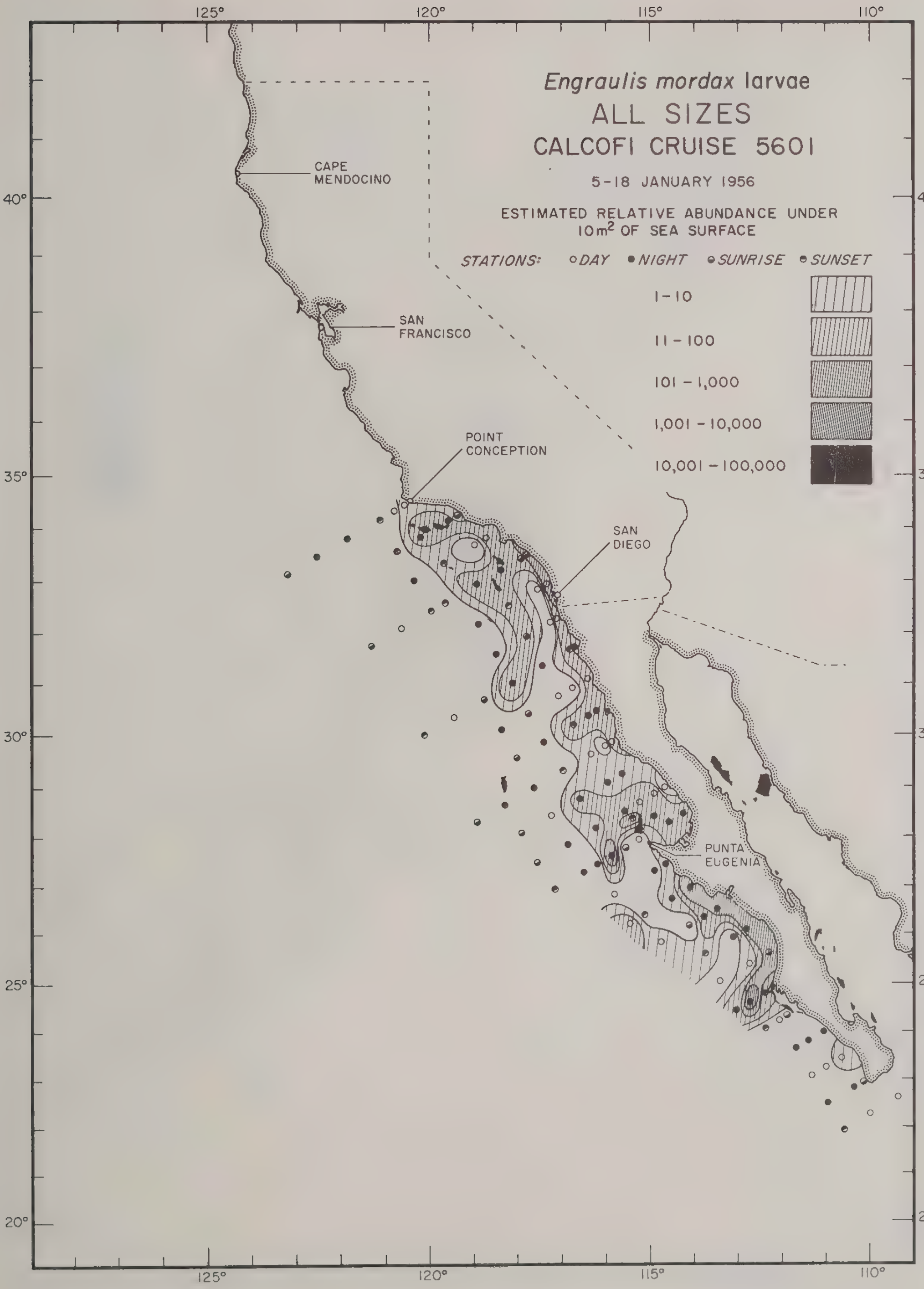
5512


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5601
5-18 JANUARY 1956
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

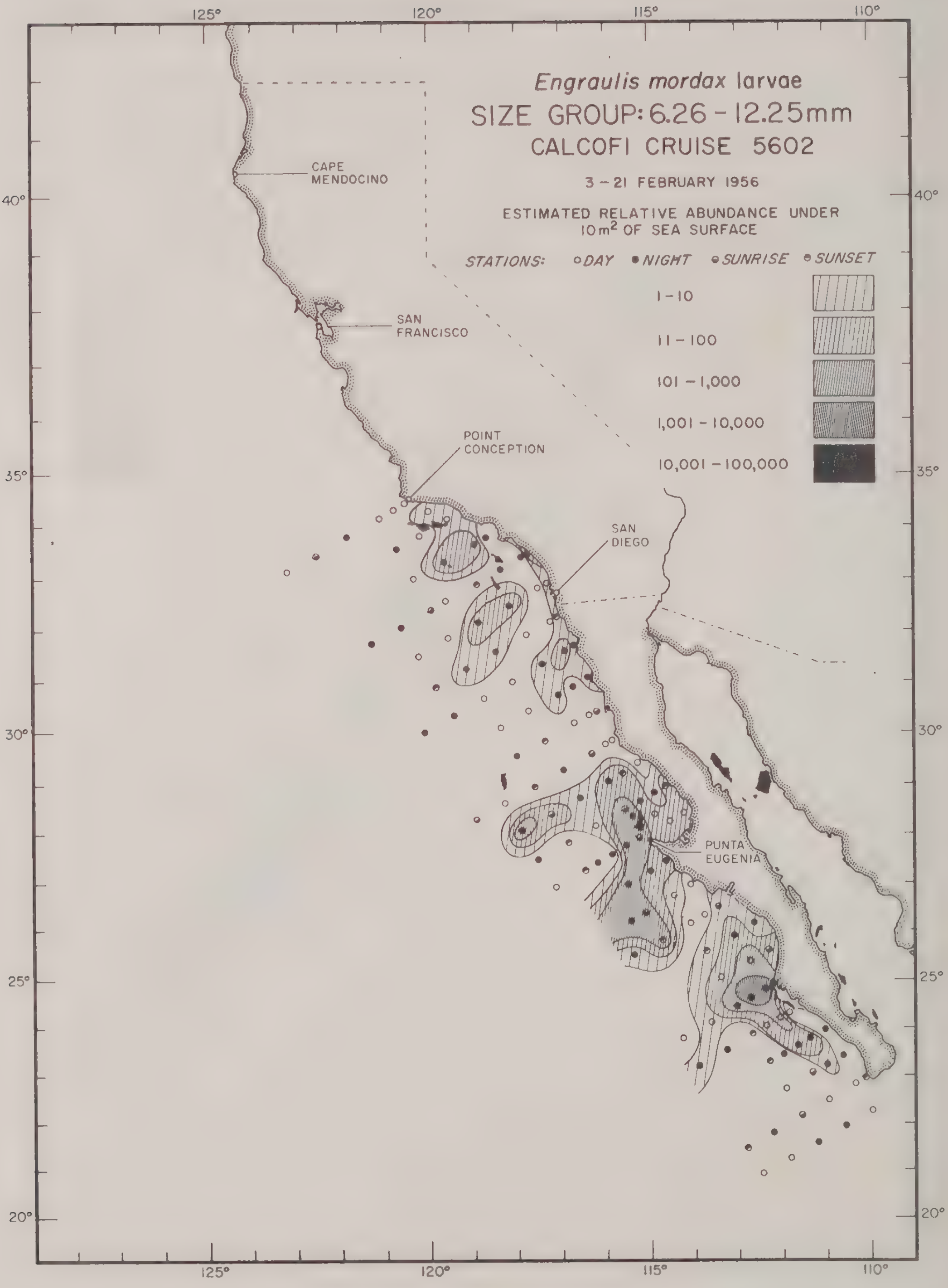
5601


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5601
5-18 JANUARY 1956
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

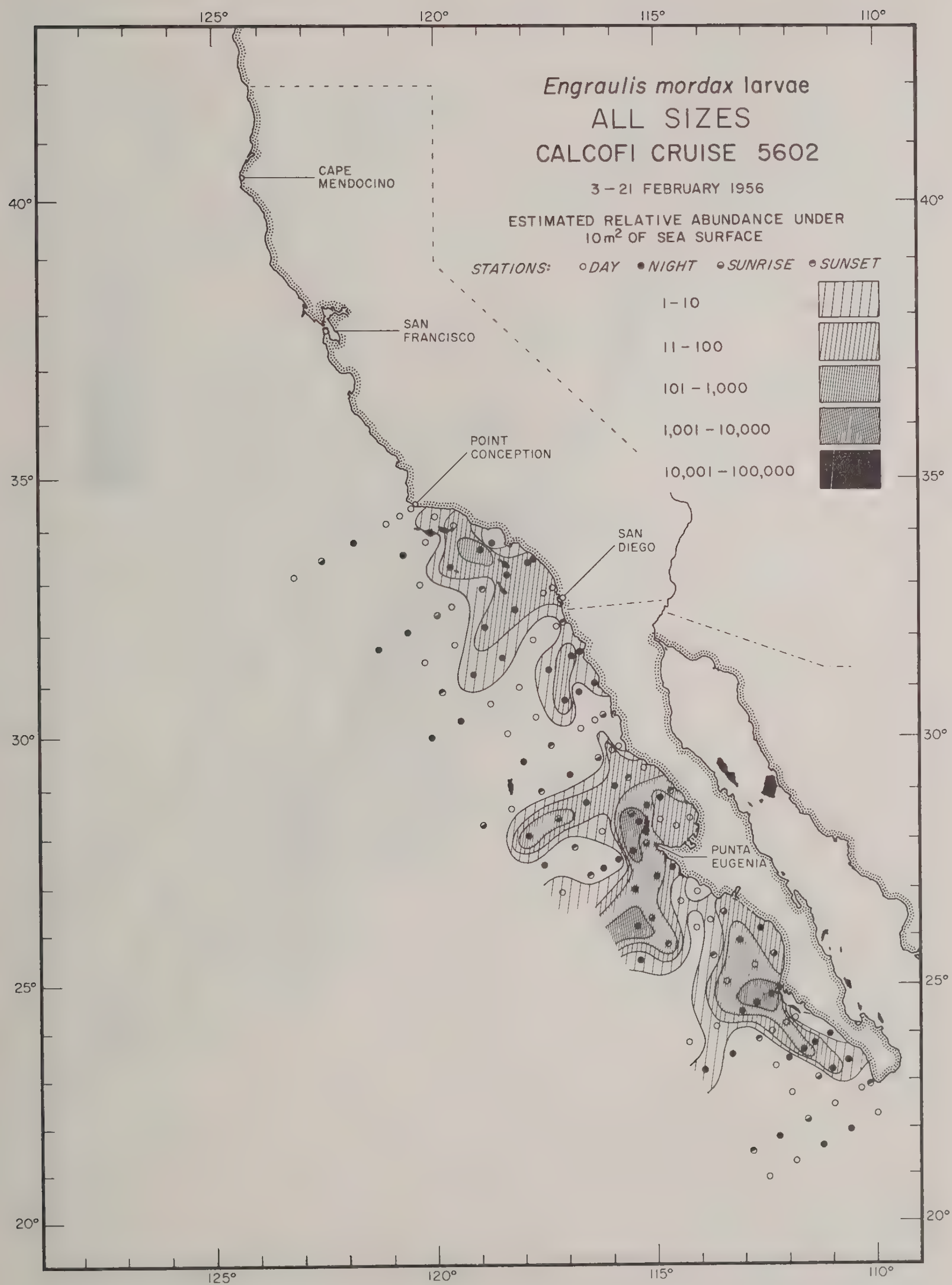
All Sizes

5601


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5602
3 - 21 FEBRUARY 1956
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◉ SUNRISE ◉ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

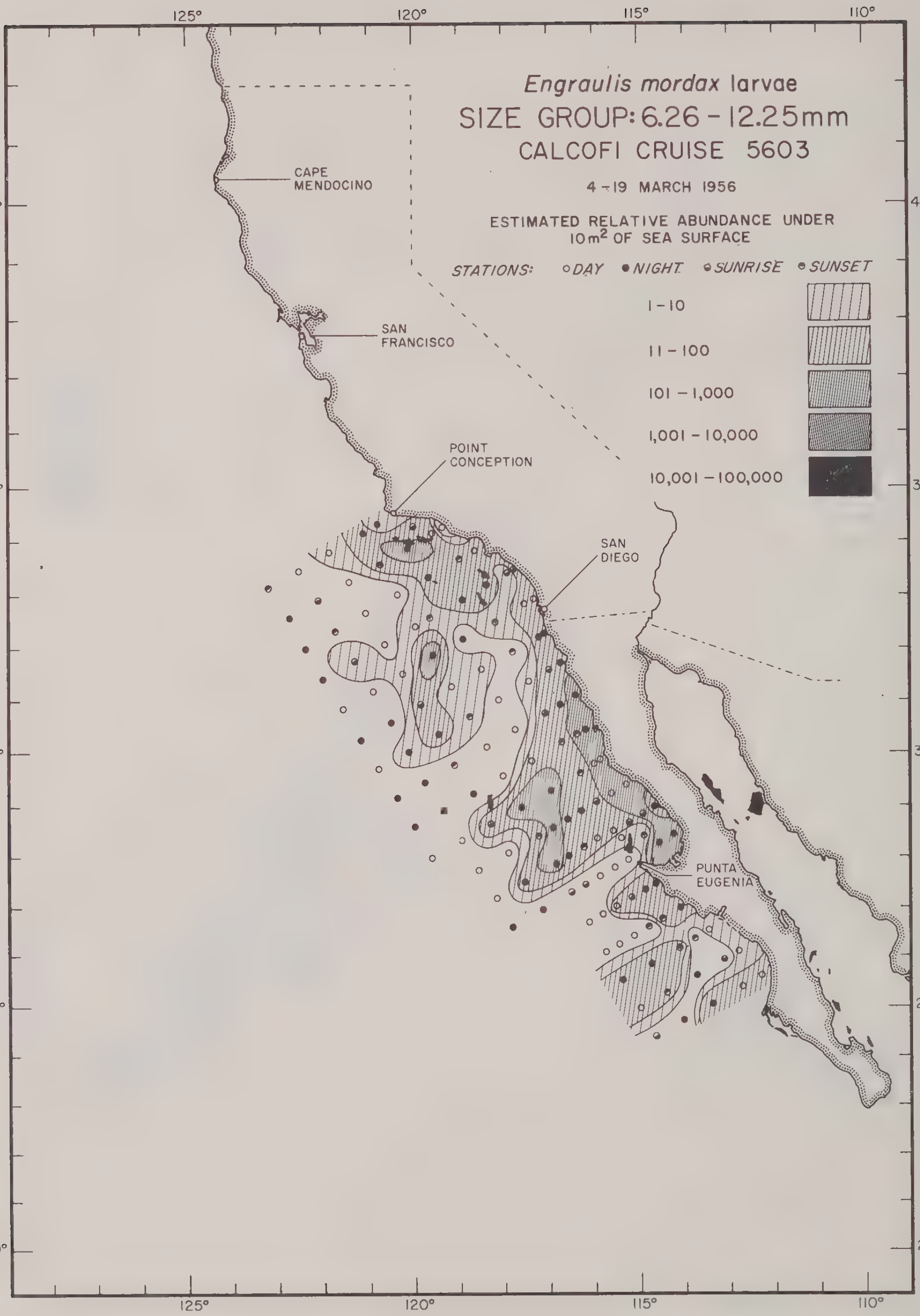
Engraulis mordax larvae

Size Group: 6.26-12.25mm
5602


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5602
3 – 21 FEBRUARY 1956
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

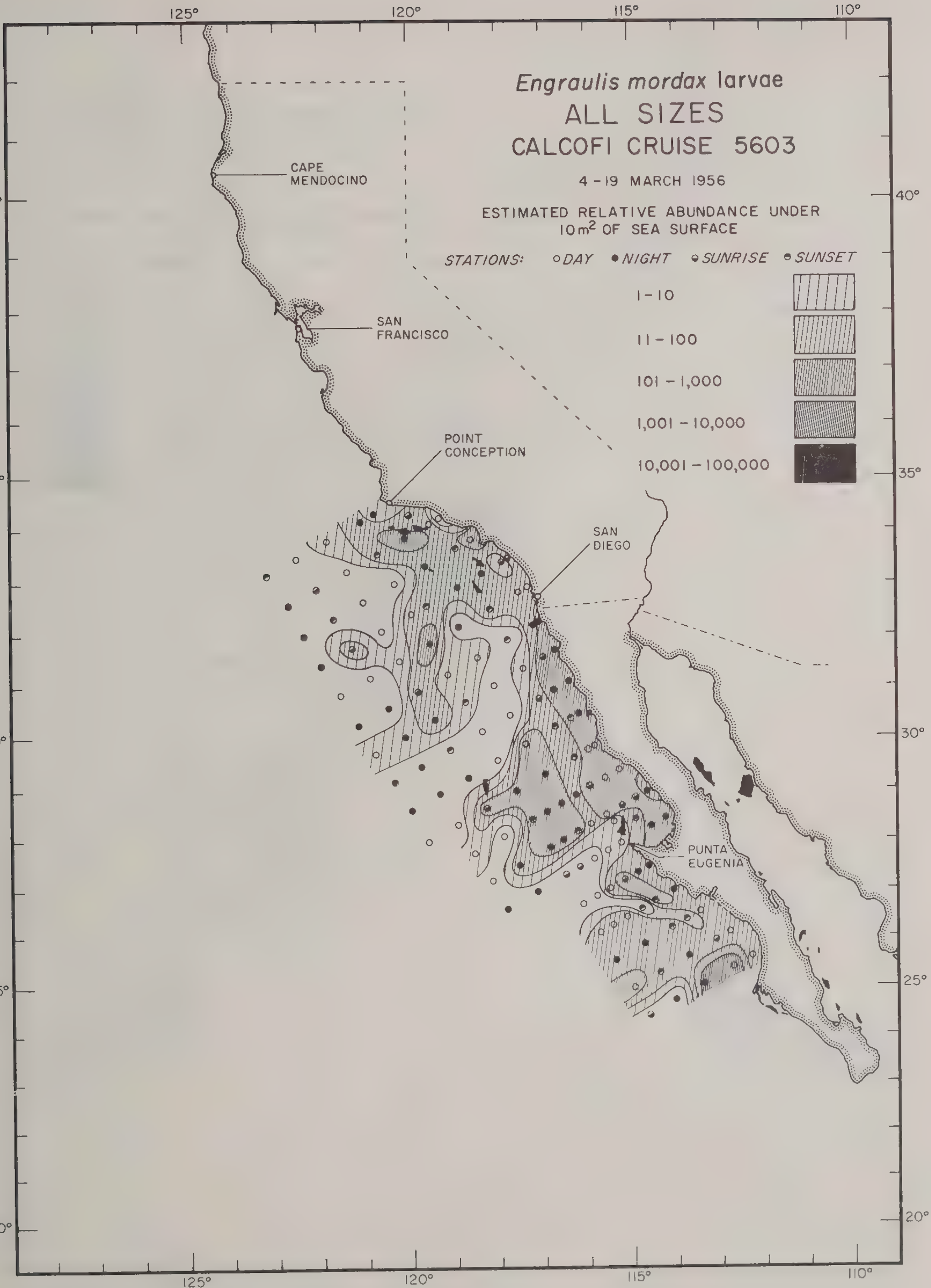
All Sizes
5602


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5603
4 - 19 MARCH 1956
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ *DAY* ● *NIGHT* *SUNRISE* *SUNSET*
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

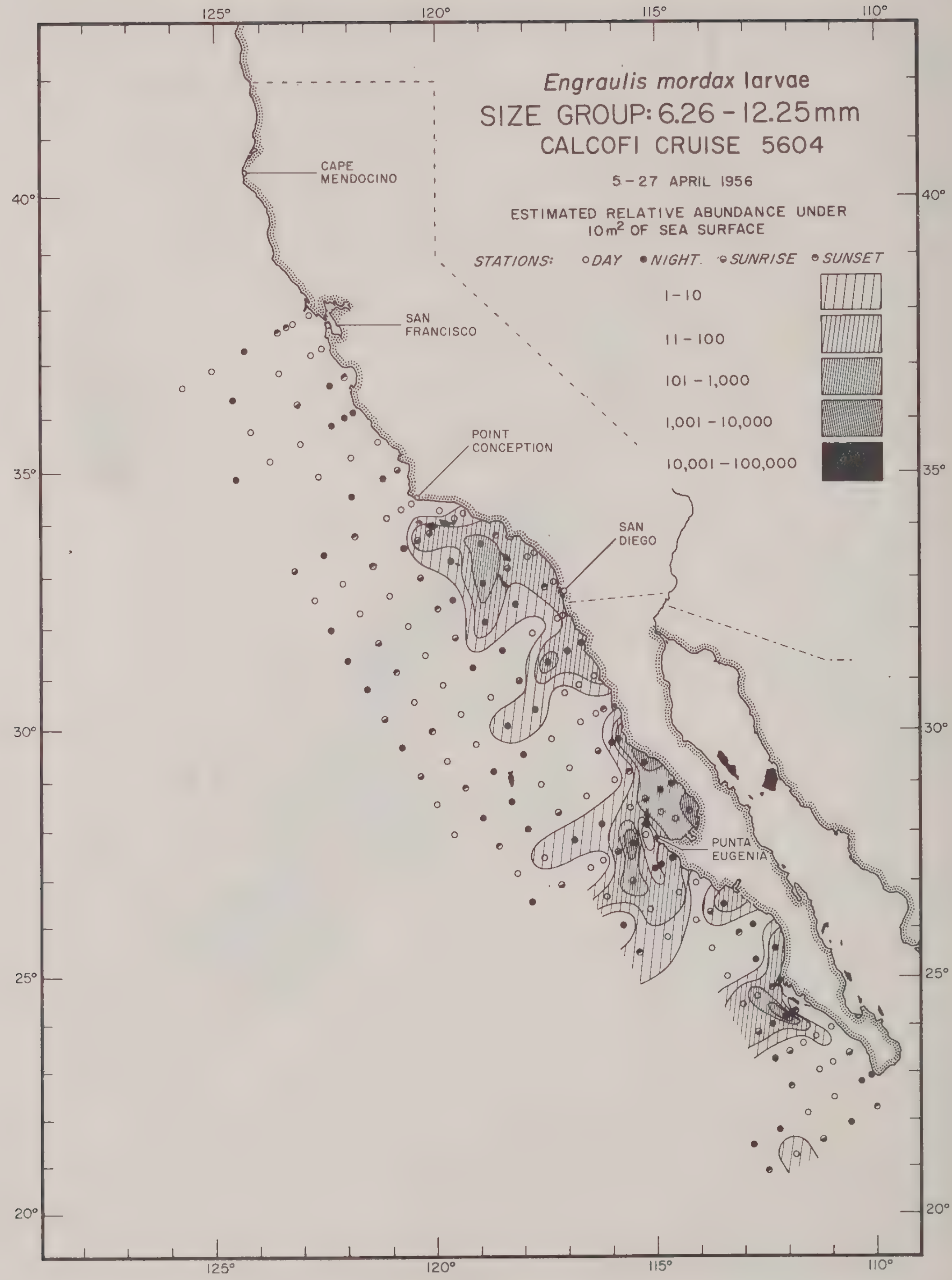
5603


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5603
4 - 19 MARCH 1956
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

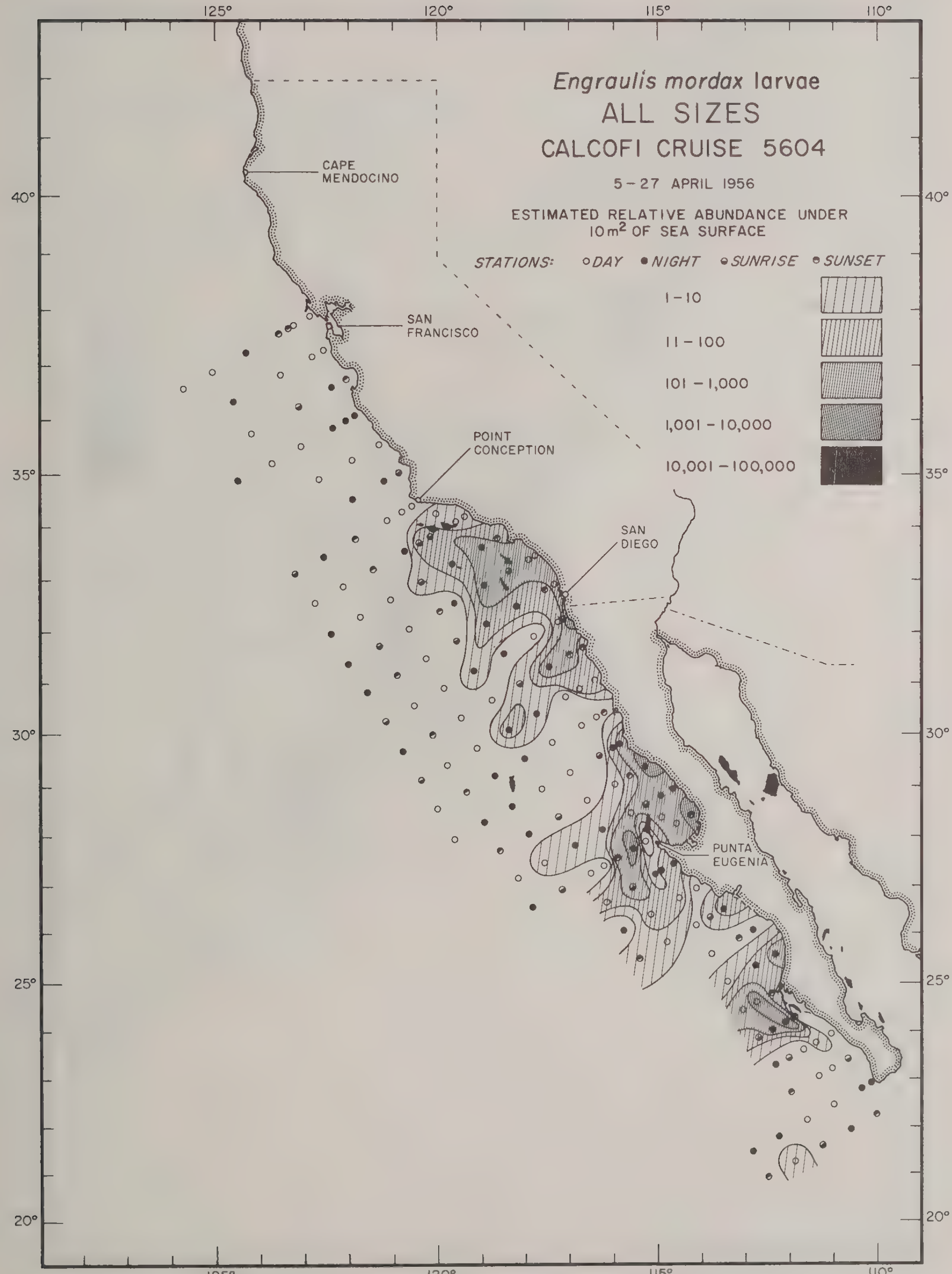
5603


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5604
5 - 27 APRIL 1956
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

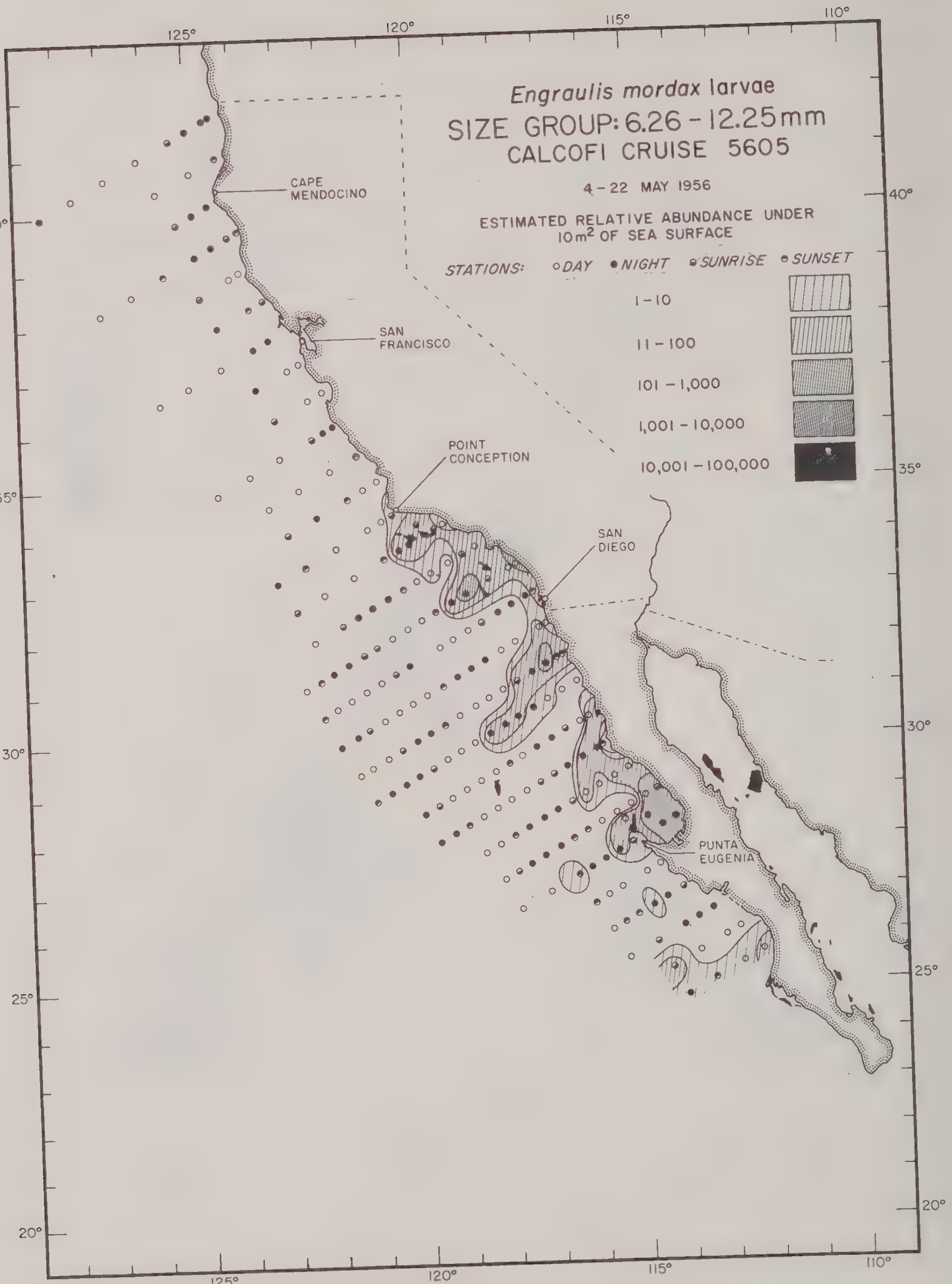
5604


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5604
5-27 APRIL 1956
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT SUNRISE SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

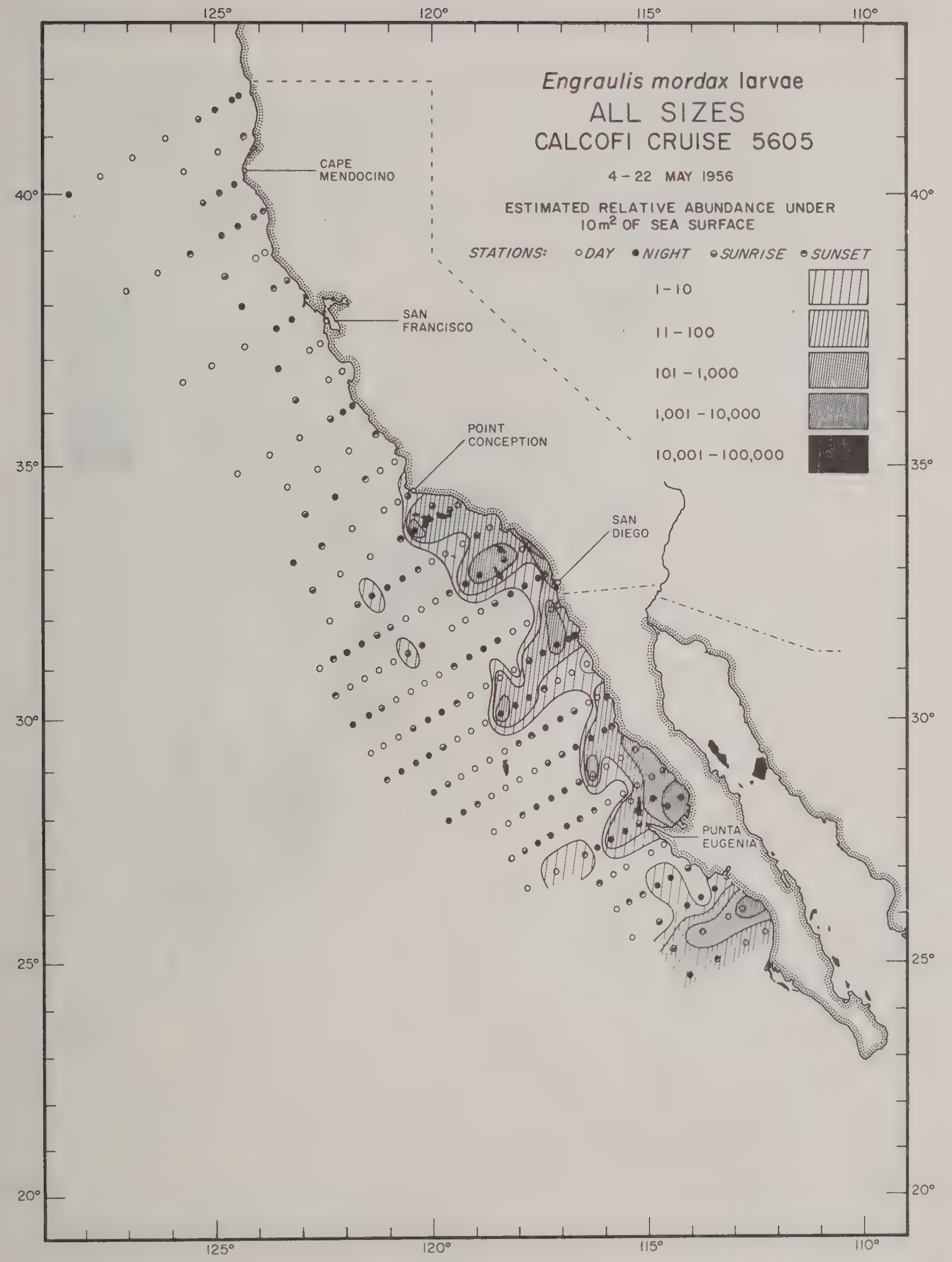
5604


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5605
4 - 22 MAY 1956
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

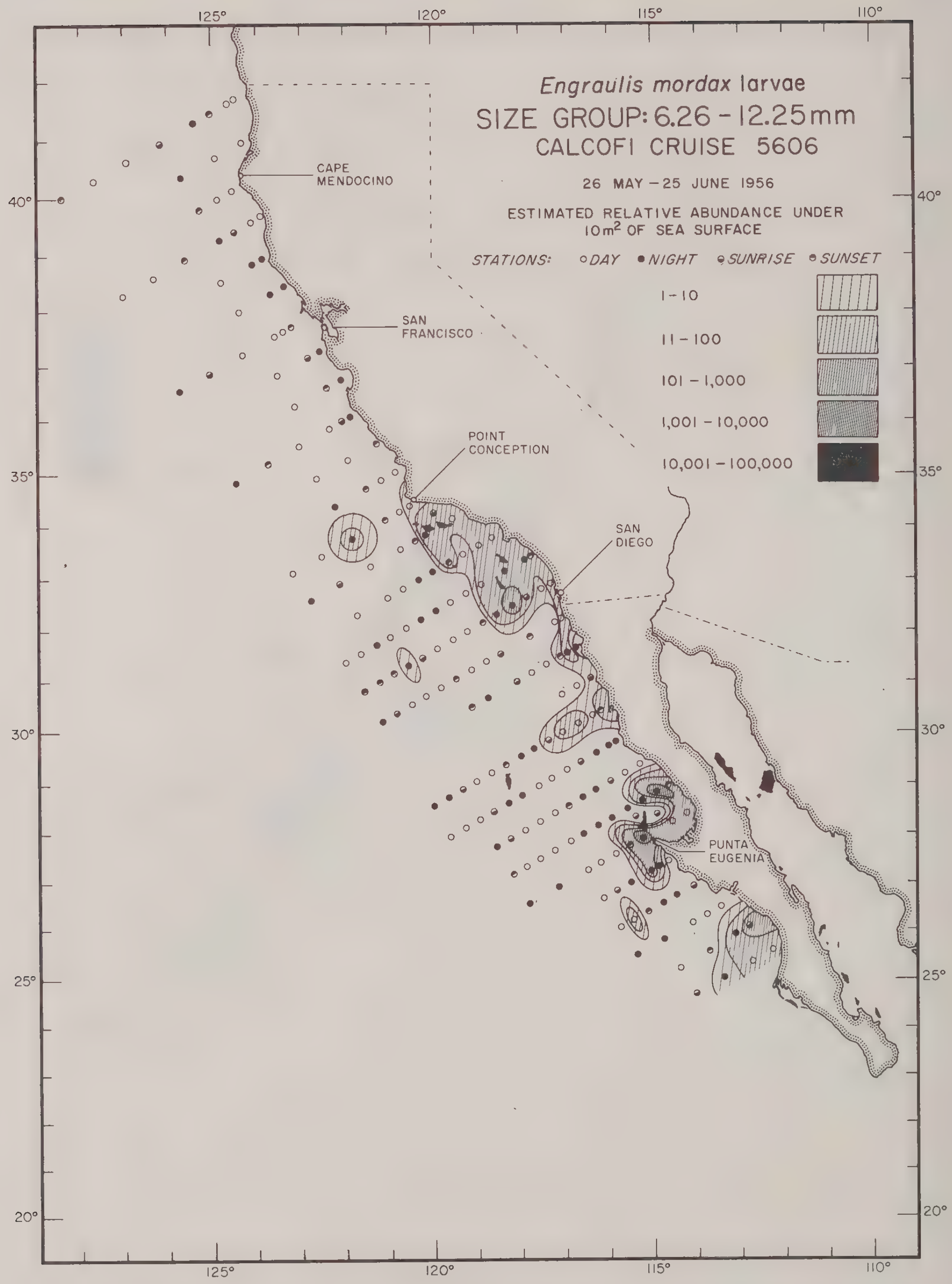
5605


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5605
4 - 22 MAY 1956
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ●SUNRISE ●SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

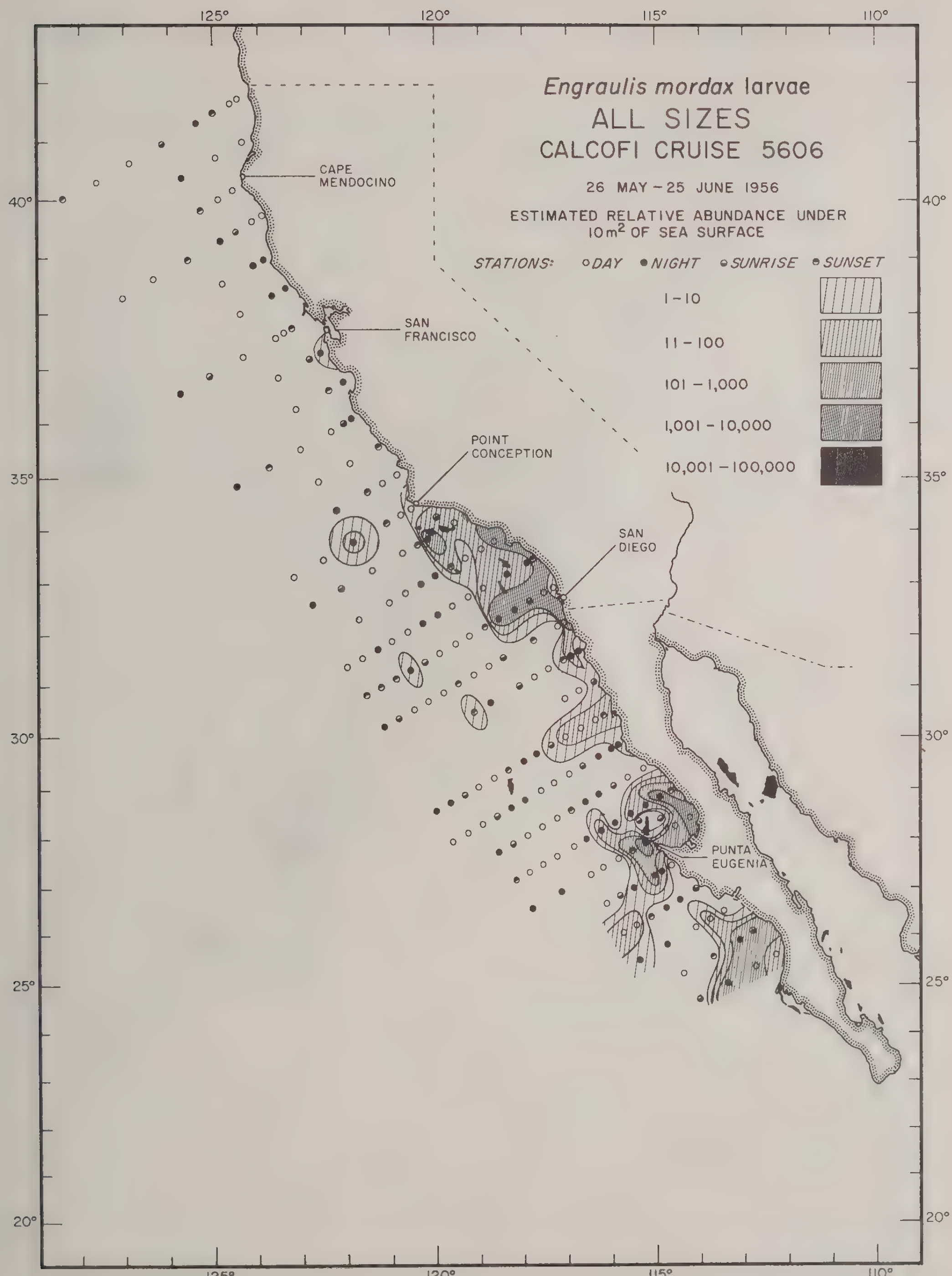
5605


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5606
26 MAY – 25 JUNE 1956
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

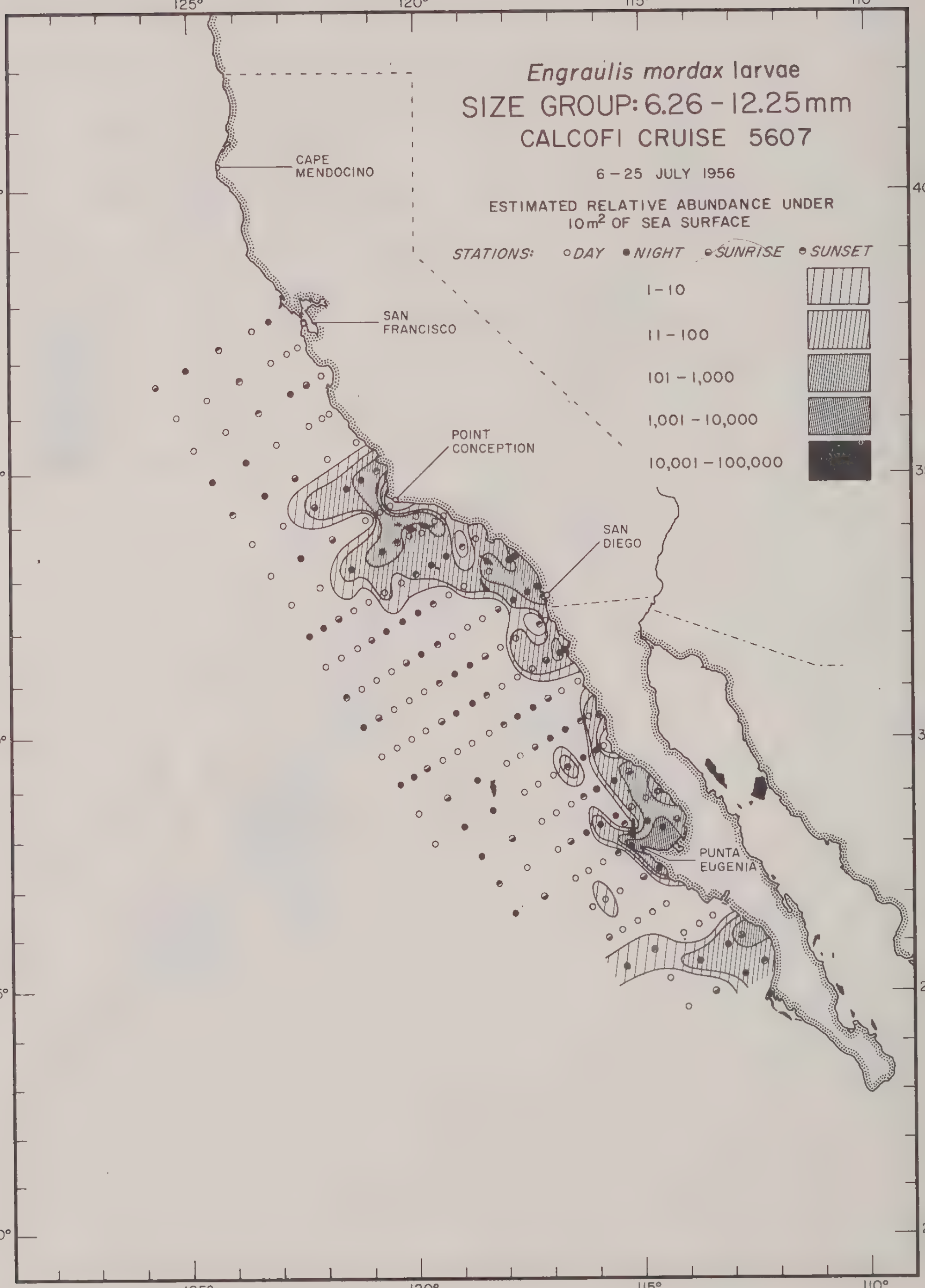
Size Group: 6.26-12.25mm

5606


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5606
26 MAY – 25 JUNE 1956
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

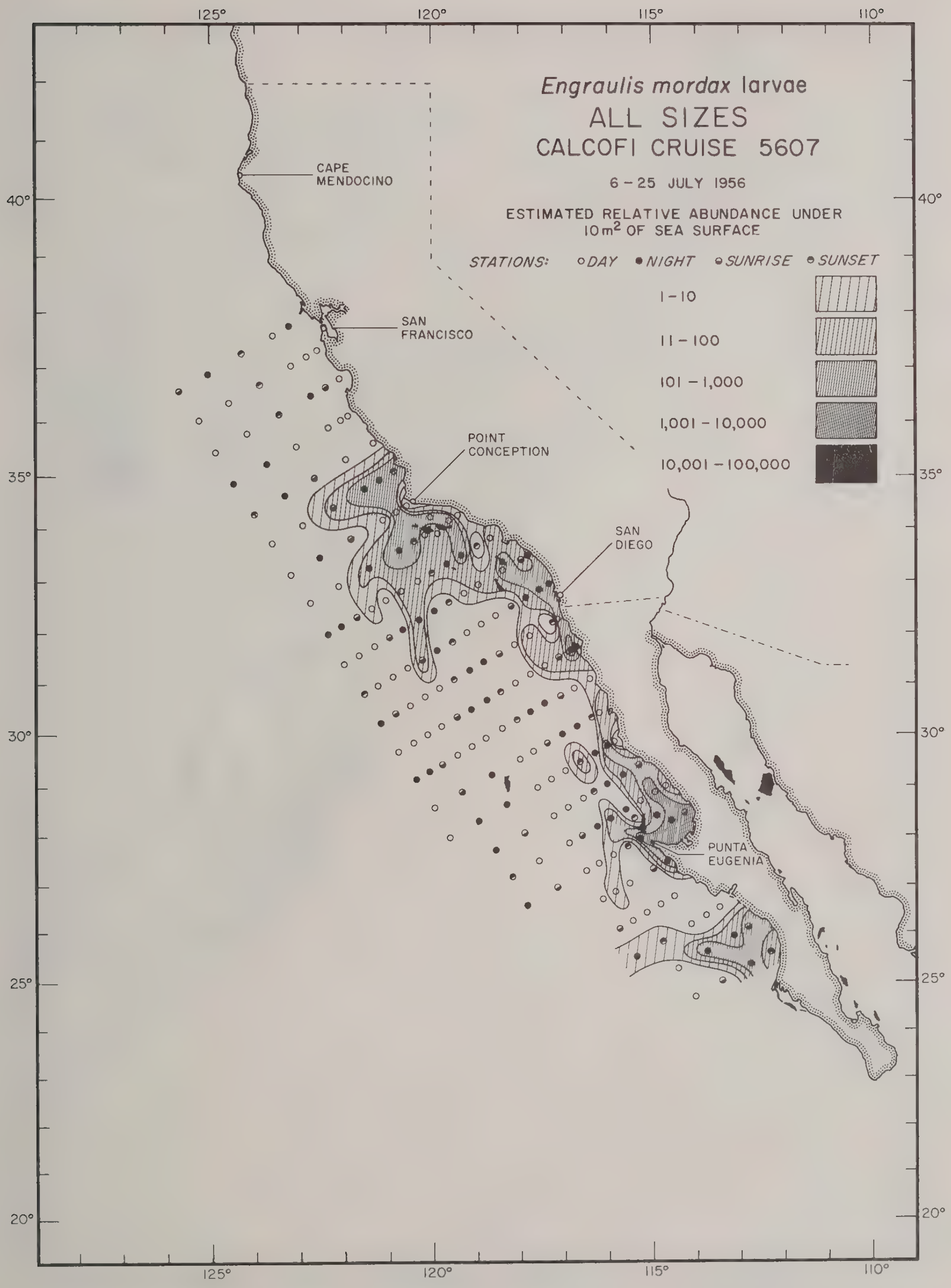
All Sizes
5606


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5607
6 – 25 JULY 1956
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

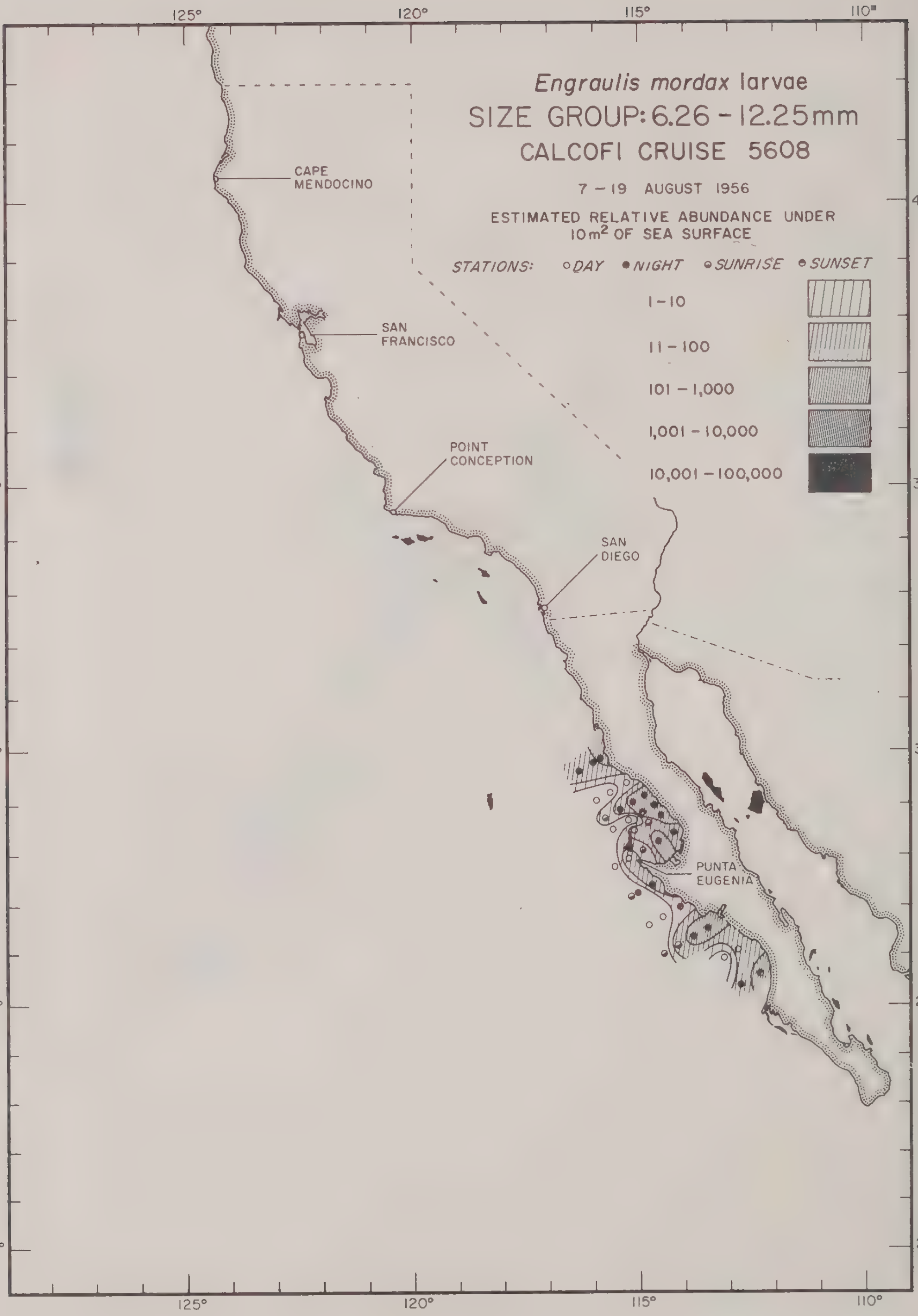
5607


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5607
6 – 25 JULY 1956
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

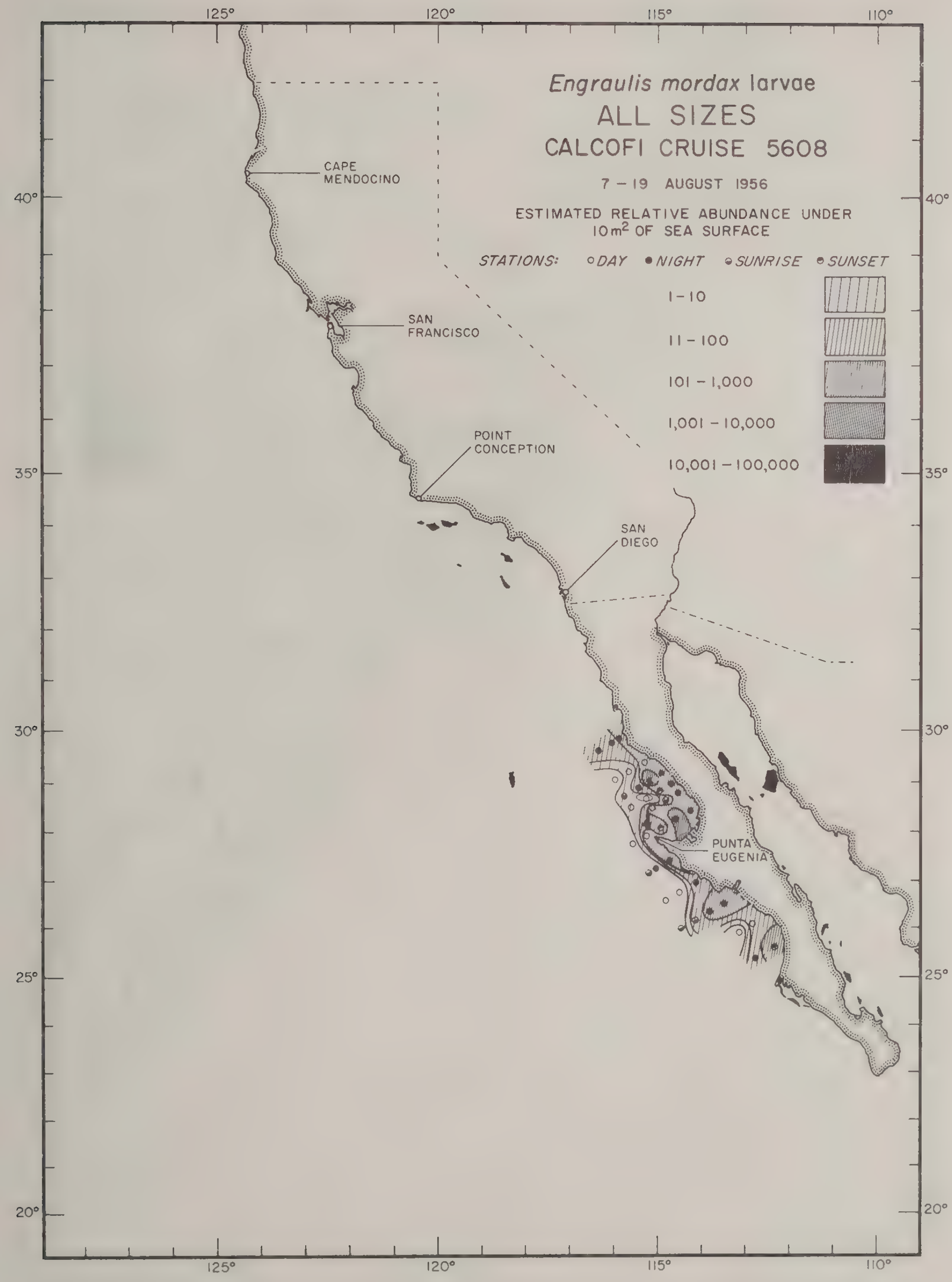
5607


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5608
7 - 19 AUGUST 1956
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◉ SUNRISE ◉ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

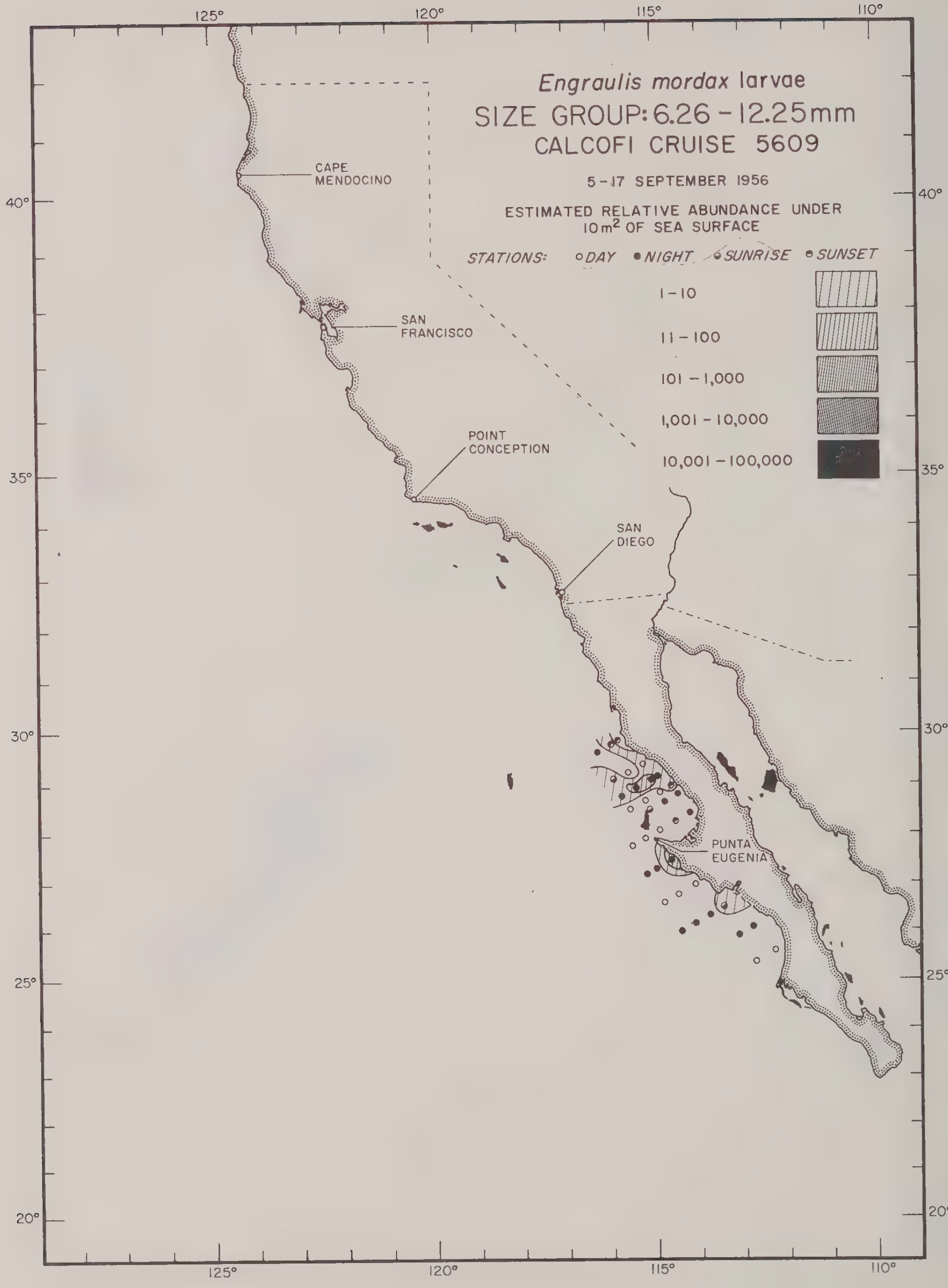
Size Group: 6.26-12.25mm

5608


125°
120°
115°
110°
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5608
7 – 19 AUGUST 1956
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
40°
35°
30°
25°
20°

Engraulis mordax larvae

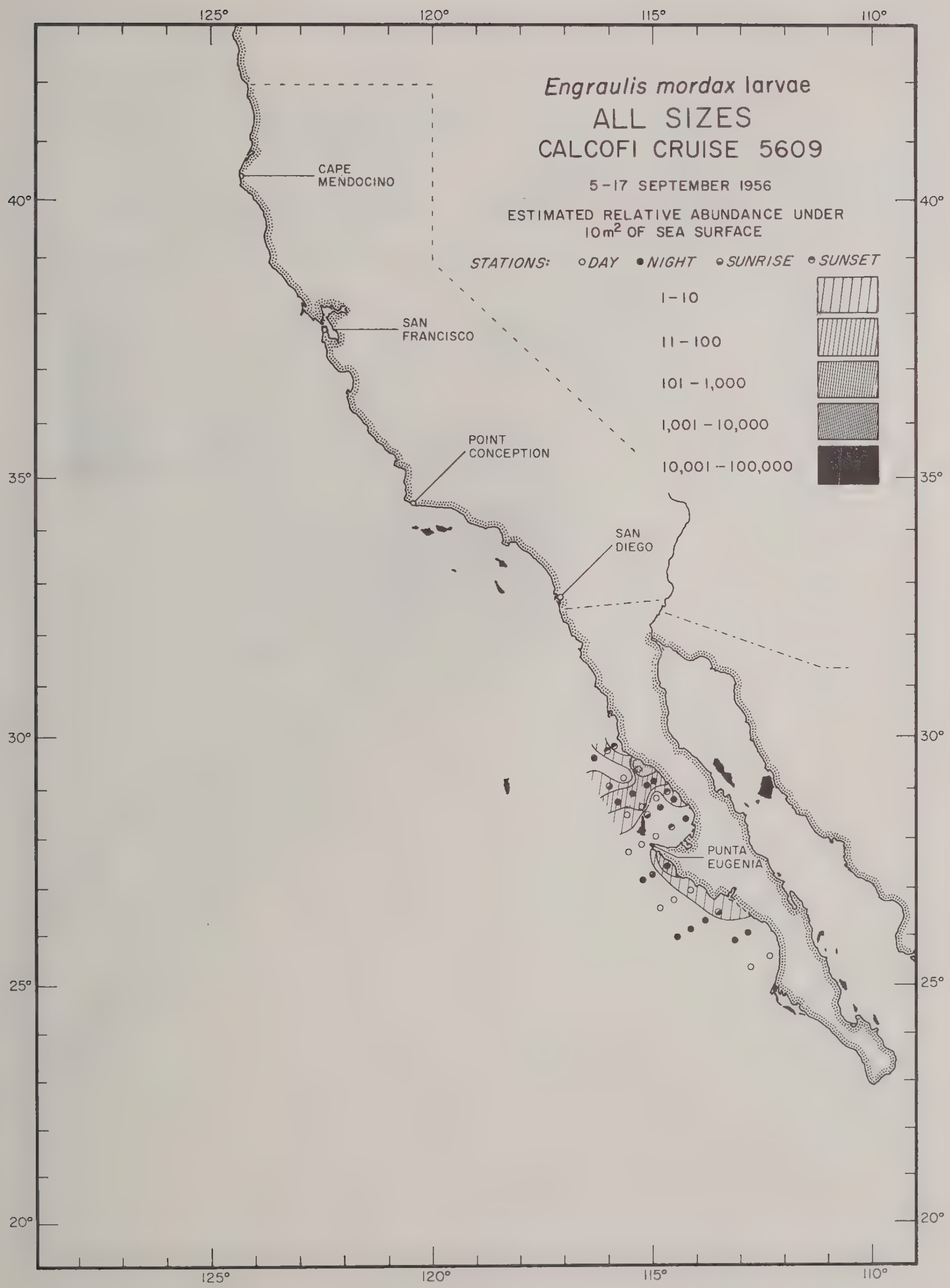
All Sizes
5608


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5609
5-17 SEPTEMBER 1956
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

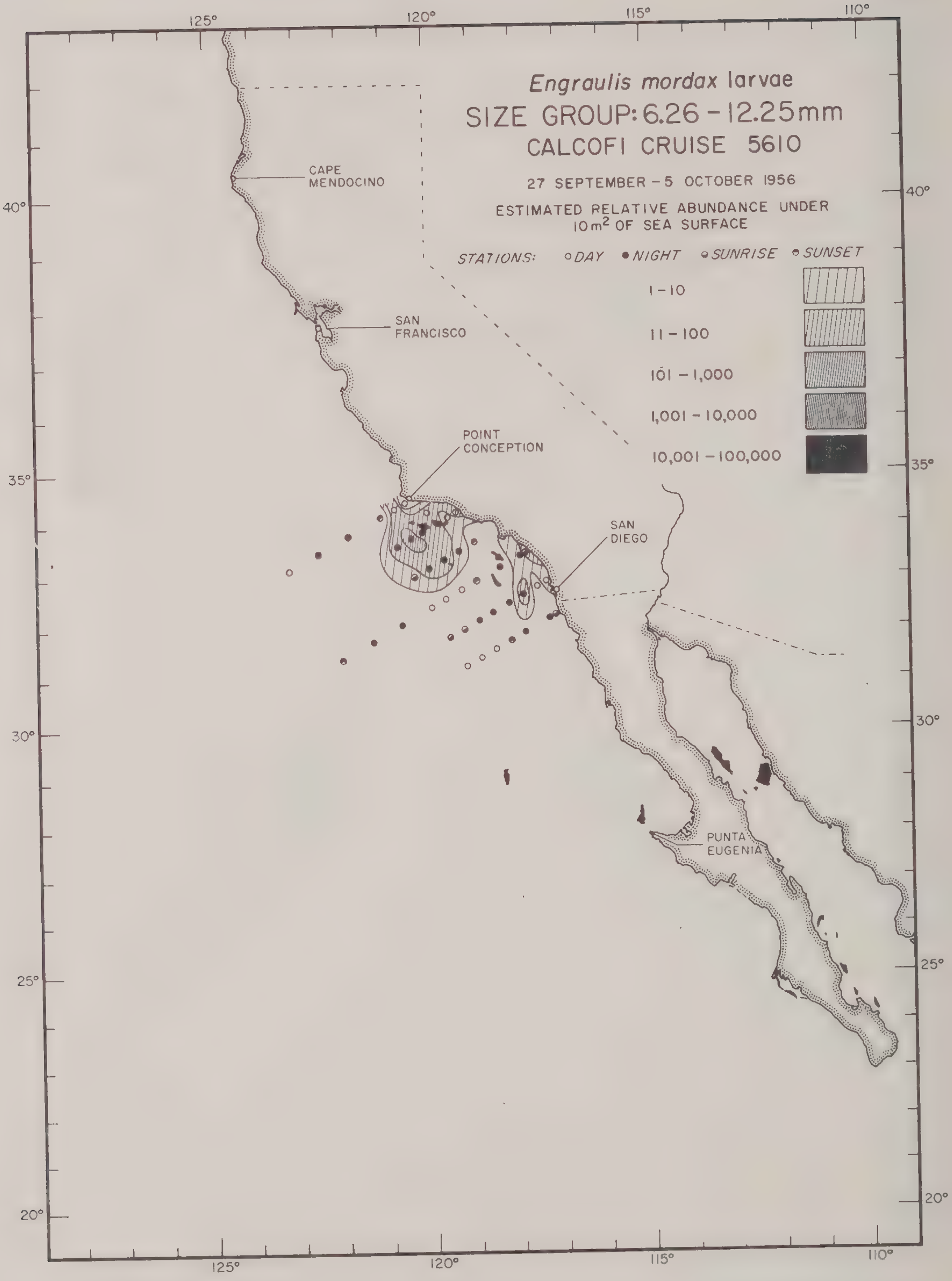
Size Group: 6.26-12.25mm

5609


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5609
5-17 SEPTEMBER 1956
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

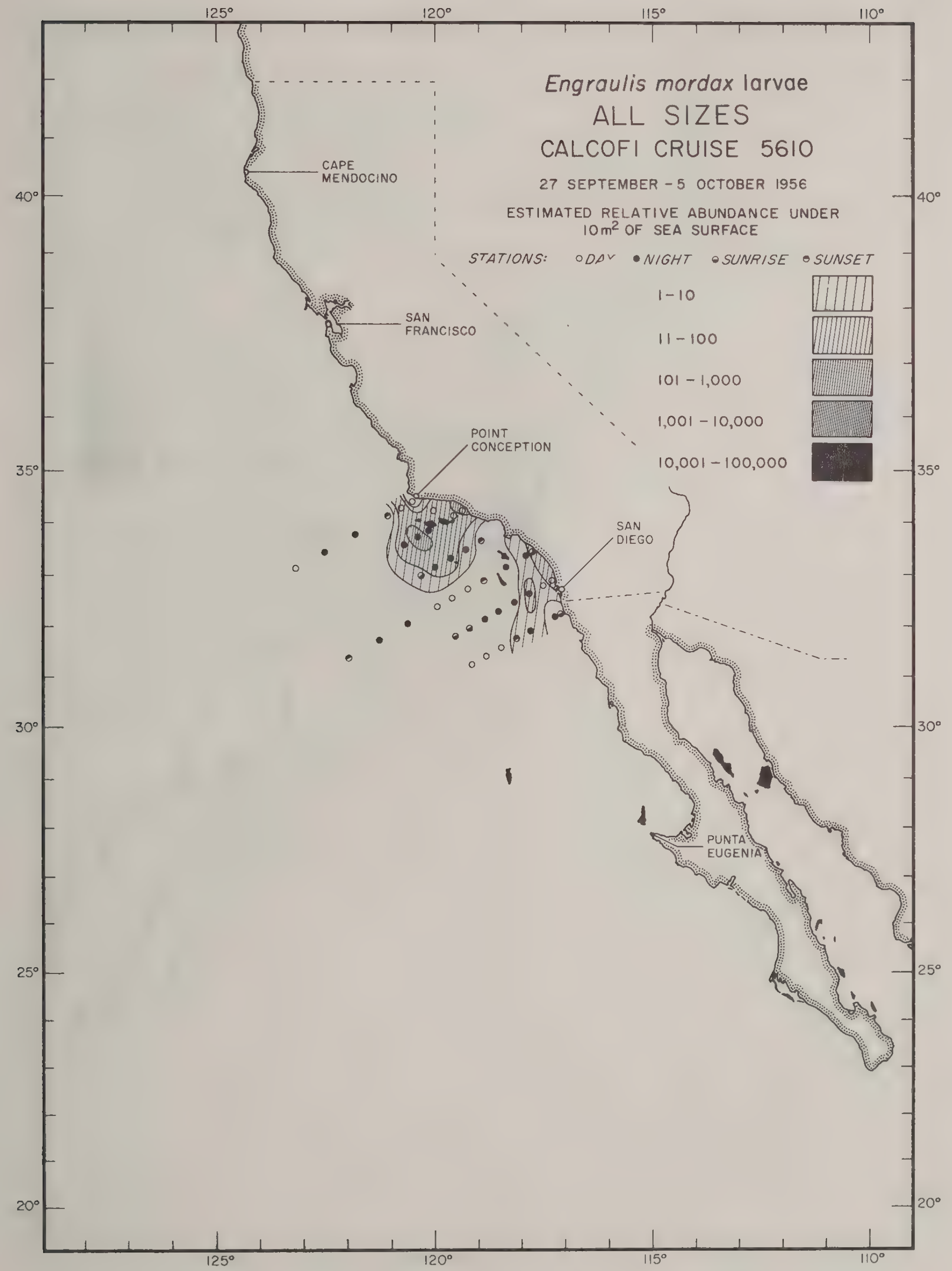
All Sizes
5609


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5610
27 SEPTEMBER - 5 OCTOBER 1956
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

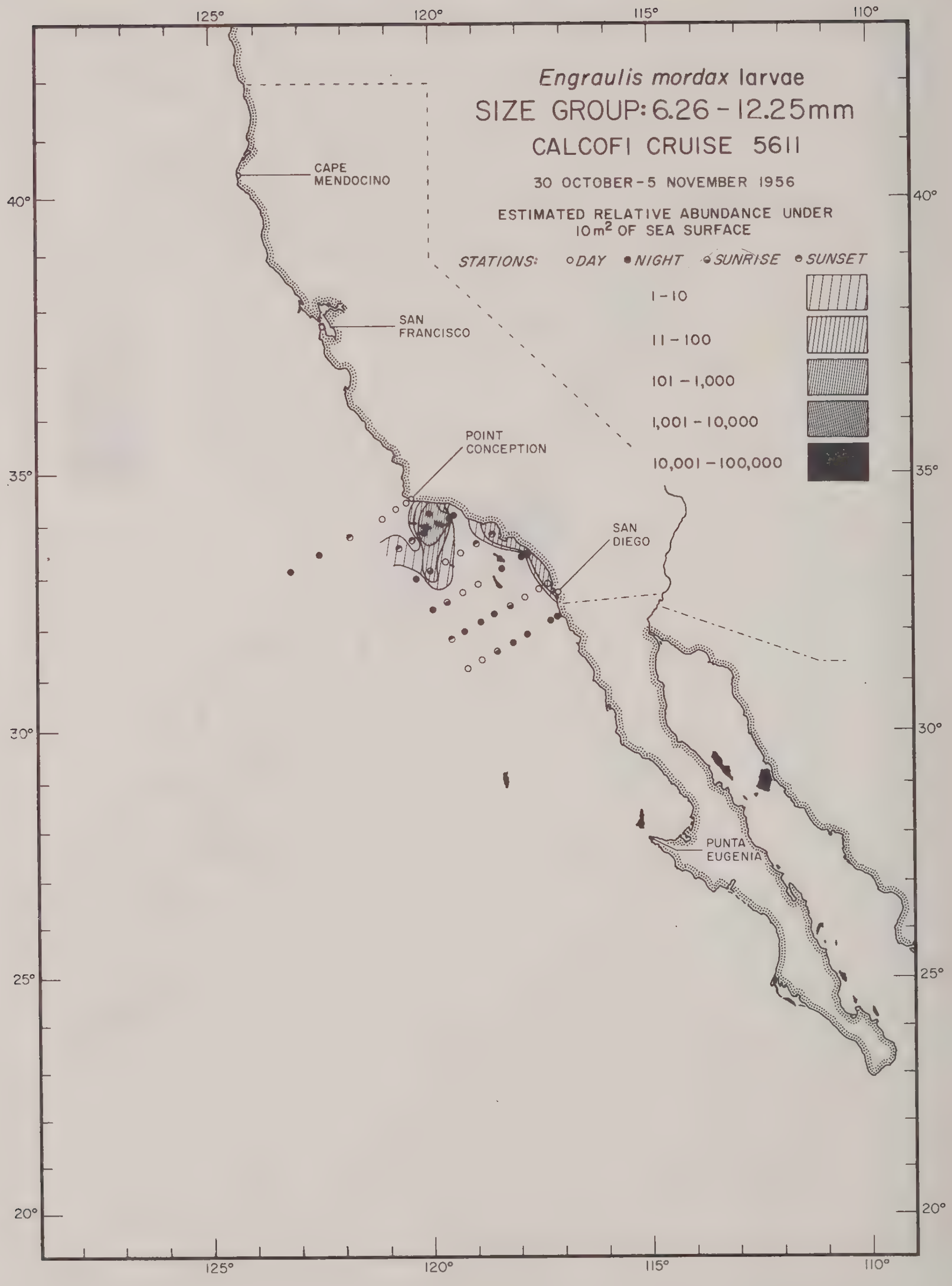
5610


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5610
27 SEPTEMBER - 5 OCTOBER 1956
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

All Sizes

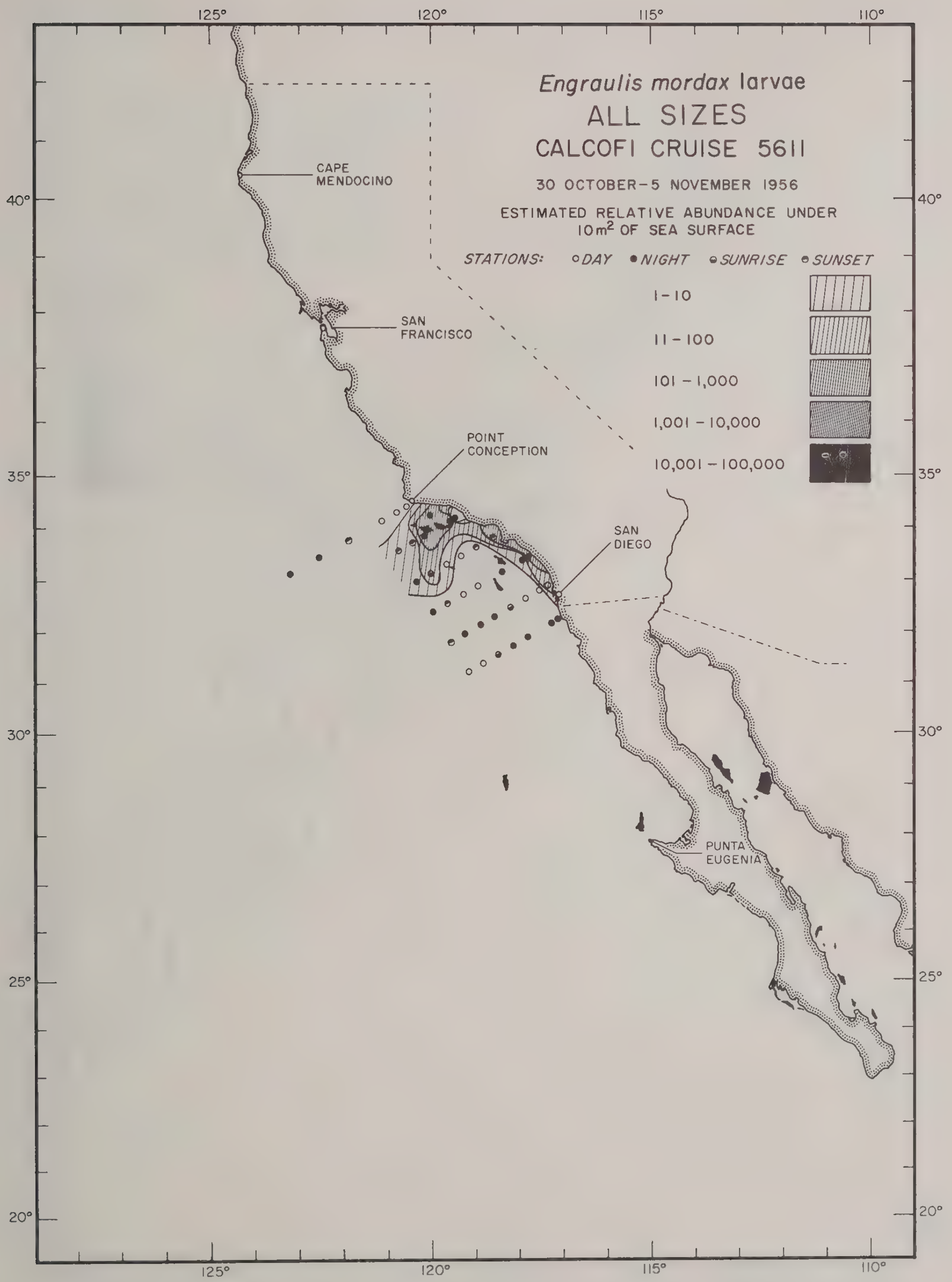
5610


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5611
30 OCTOBER - 5 NOVEMBER 1956
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

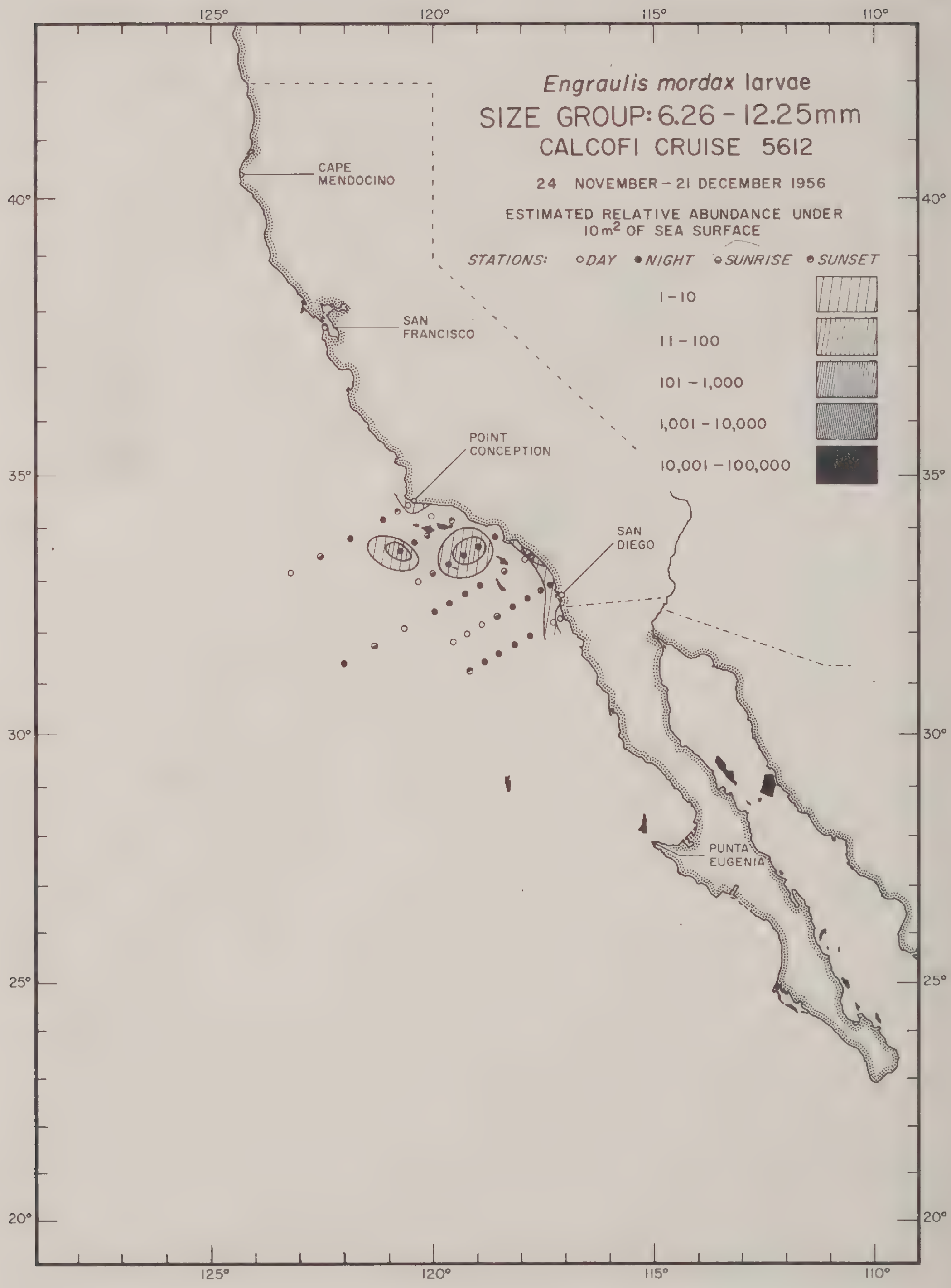
5611


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5611
30 OCTOBER–5 NOVEMBER 1956
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT SUNRISE SUNSET
1–10
11–100
101–1,000
1,001–10,000
10,001–100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

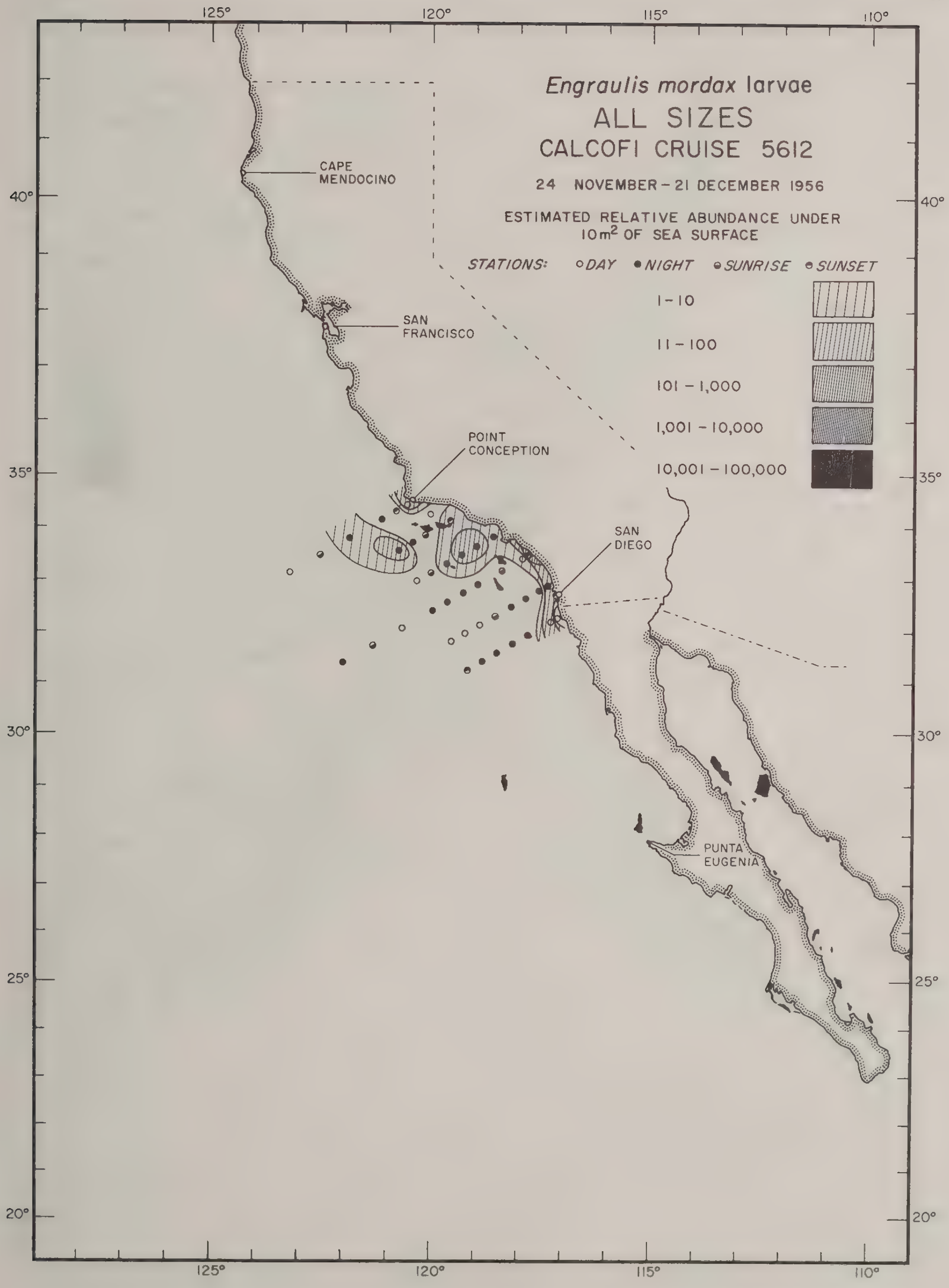
5611


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5612
24 NOVEMBER – 21 DECEMBER 1956
ESTIMATED RELATIVE ABUNDANCE UNDER 10m^2 OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◉ SUNRISE ◉ SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

Size Group: 6.26-12.25mm

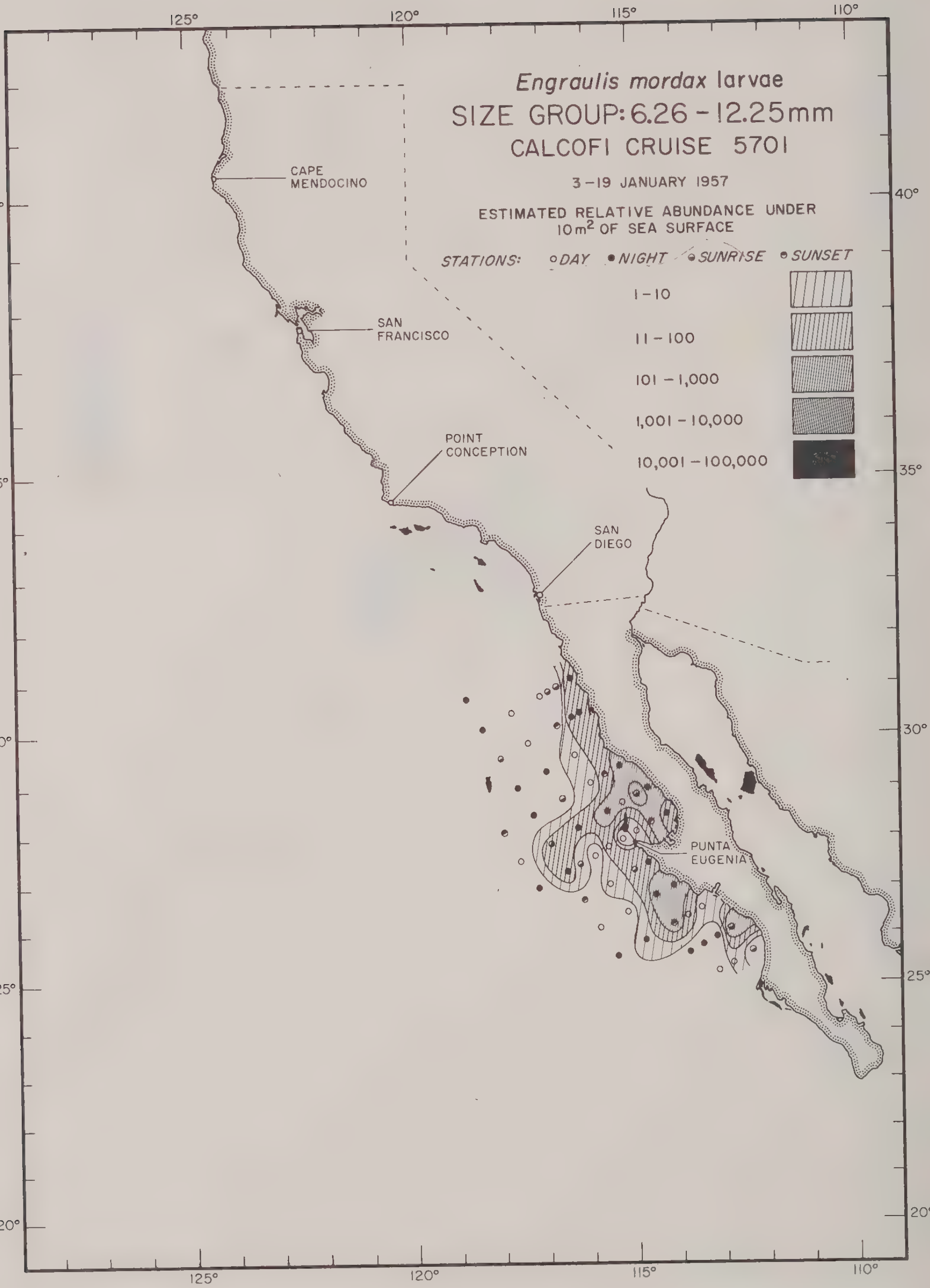
5612


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5612
24 NOVEMBER - 21 DECEMBER 1956
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◐SUNRISE ◐SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

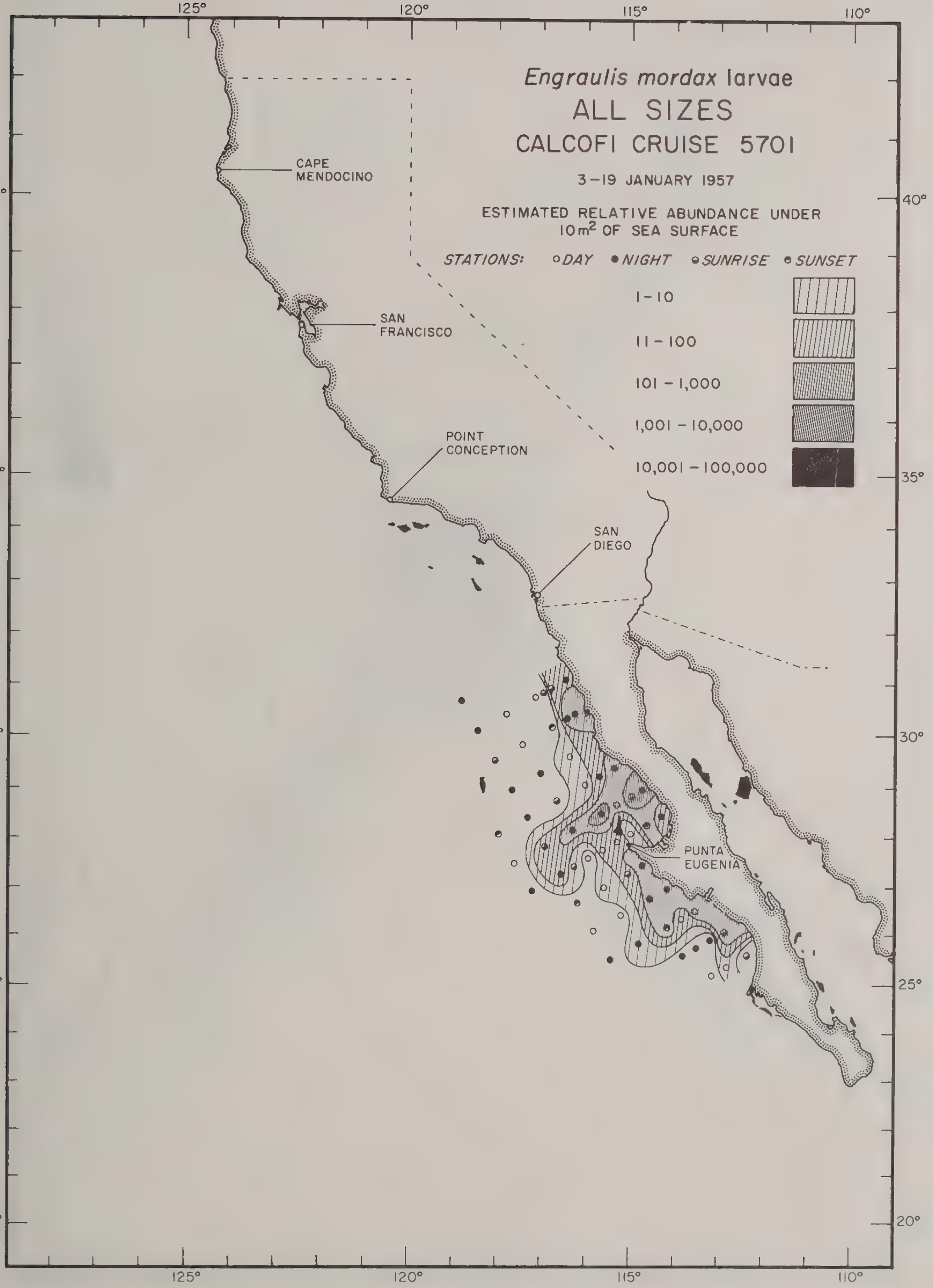
5612


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5701
3-19 JANUARY 1957
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

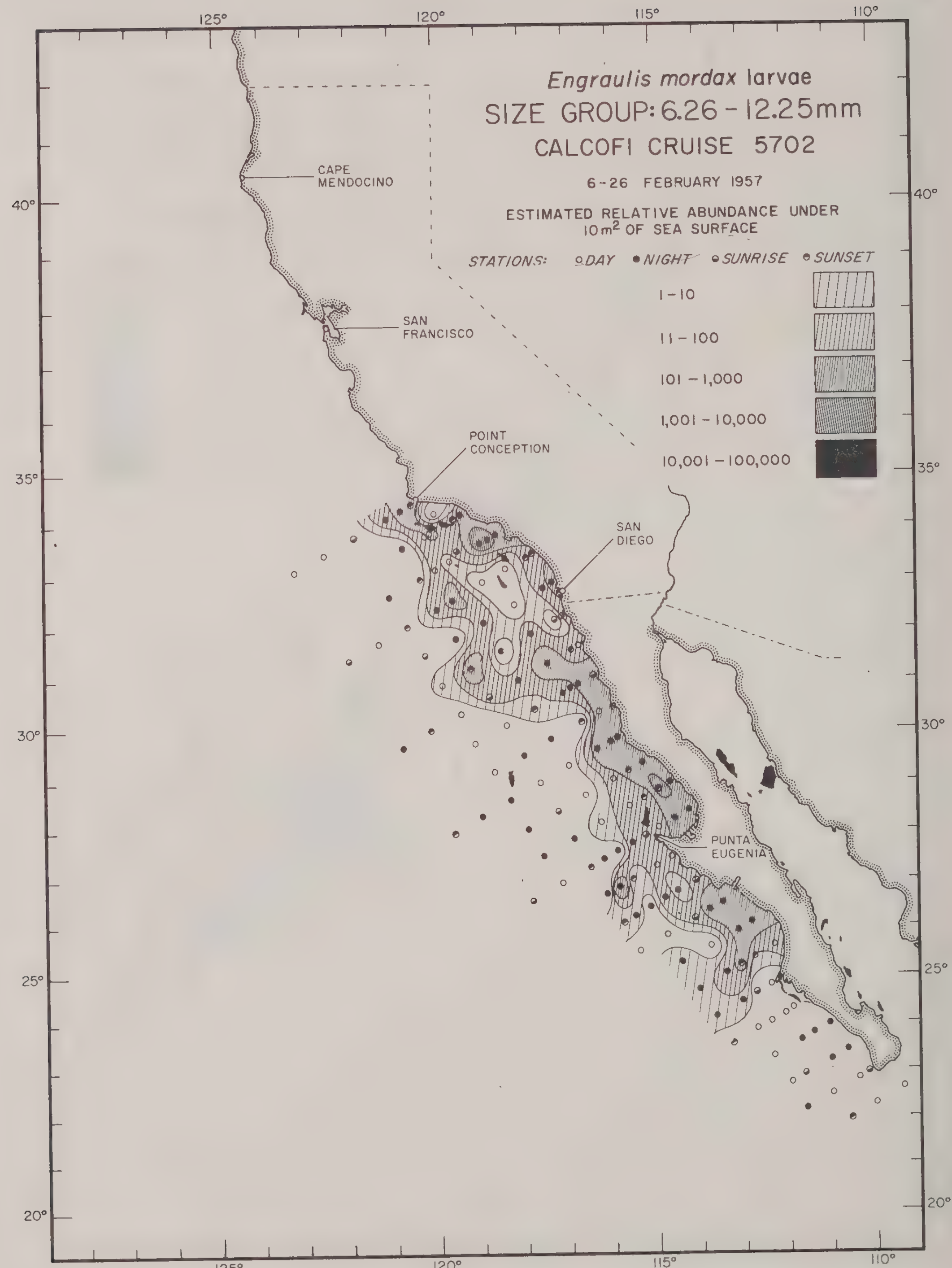
Size Group: 6.26-12.25mm

5701


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5701
3-19 JANUARY 1957
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◉SUNRISE ◉SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

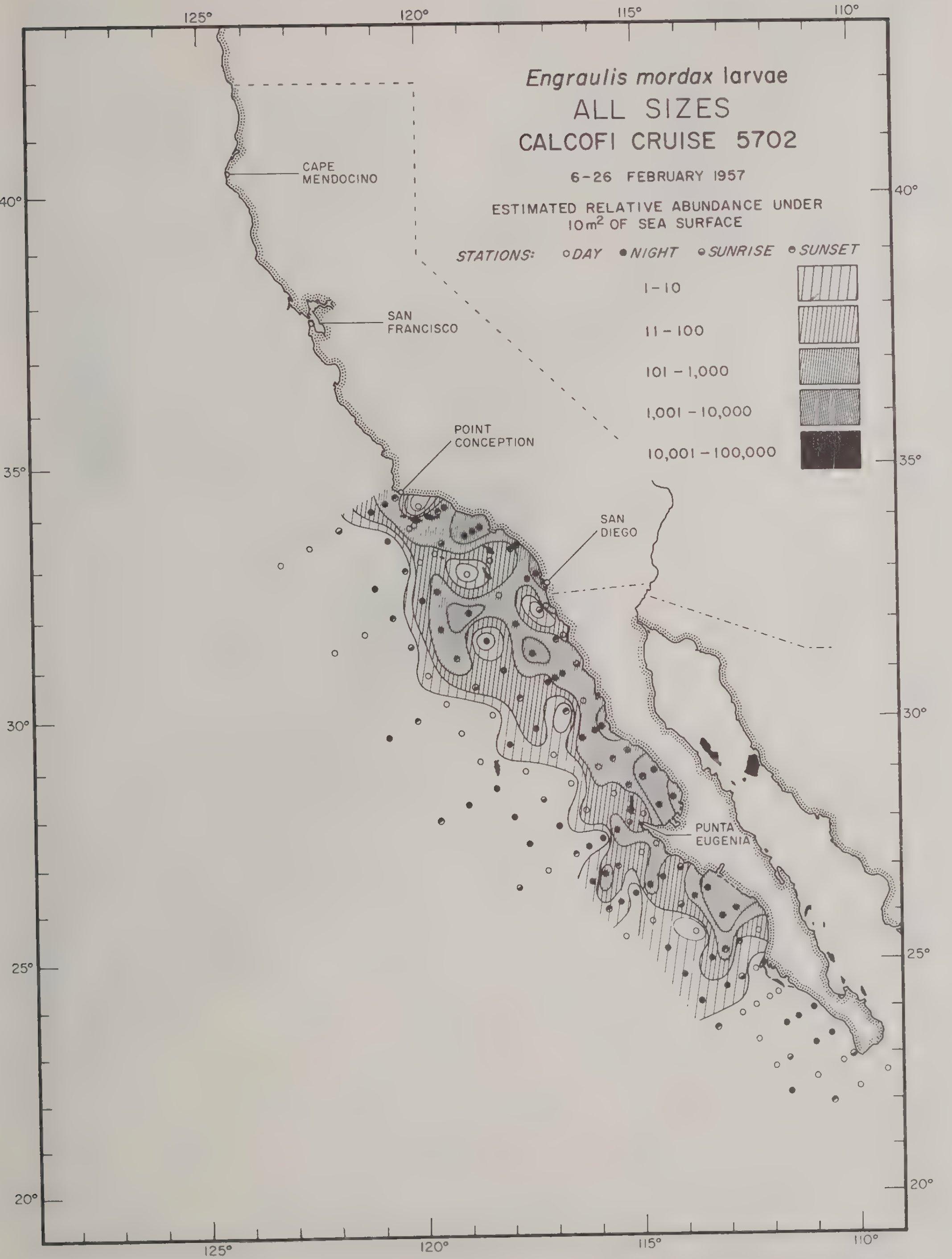
All Sizes
5701


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5702
6-26 FEBRUARY 1957
ESTIMATED RELATIVE ABUNDANCE UNDER
$10 m^2$ OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

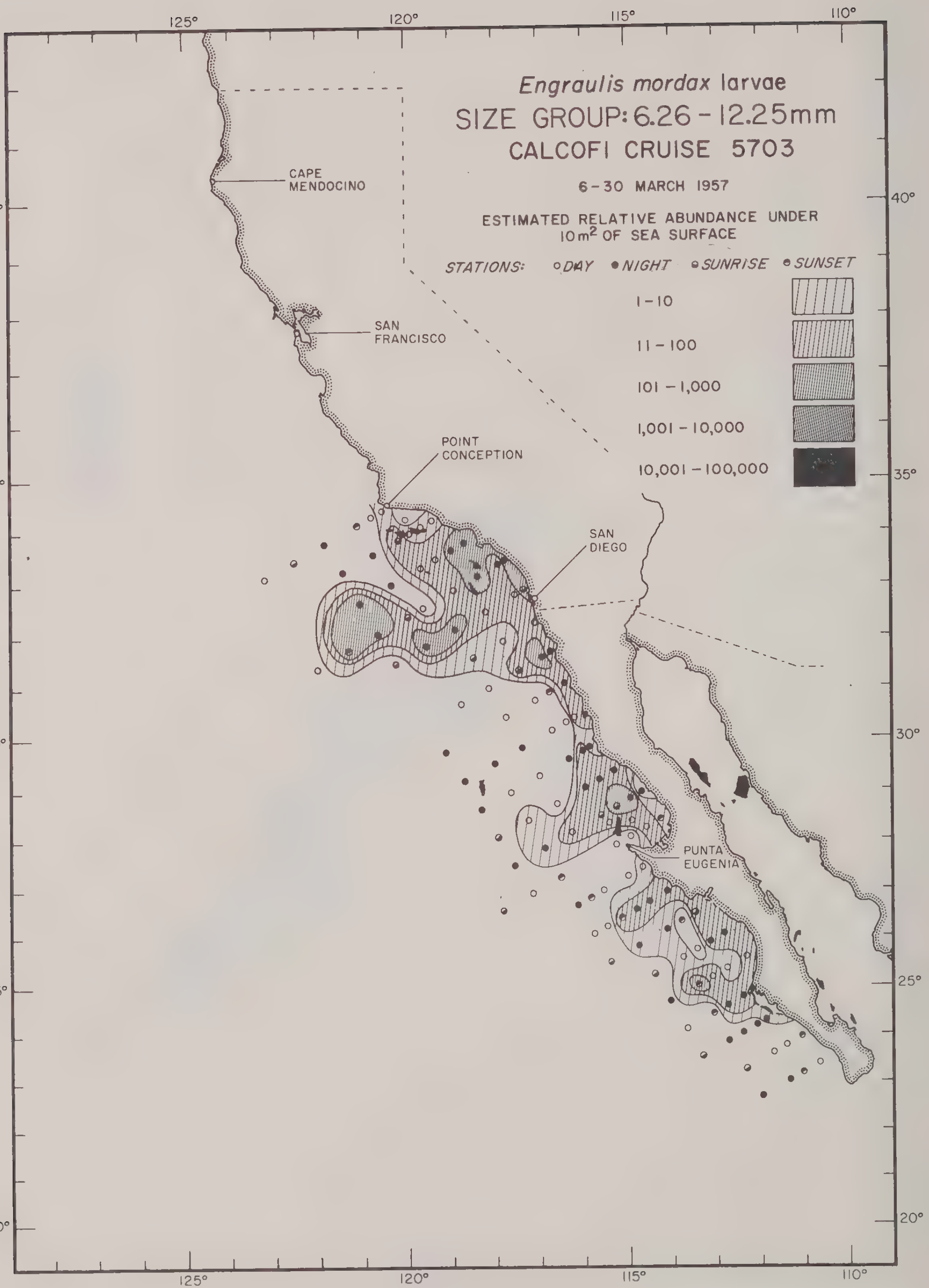
5702


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5702
6-26 FEBRUARY 1957
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

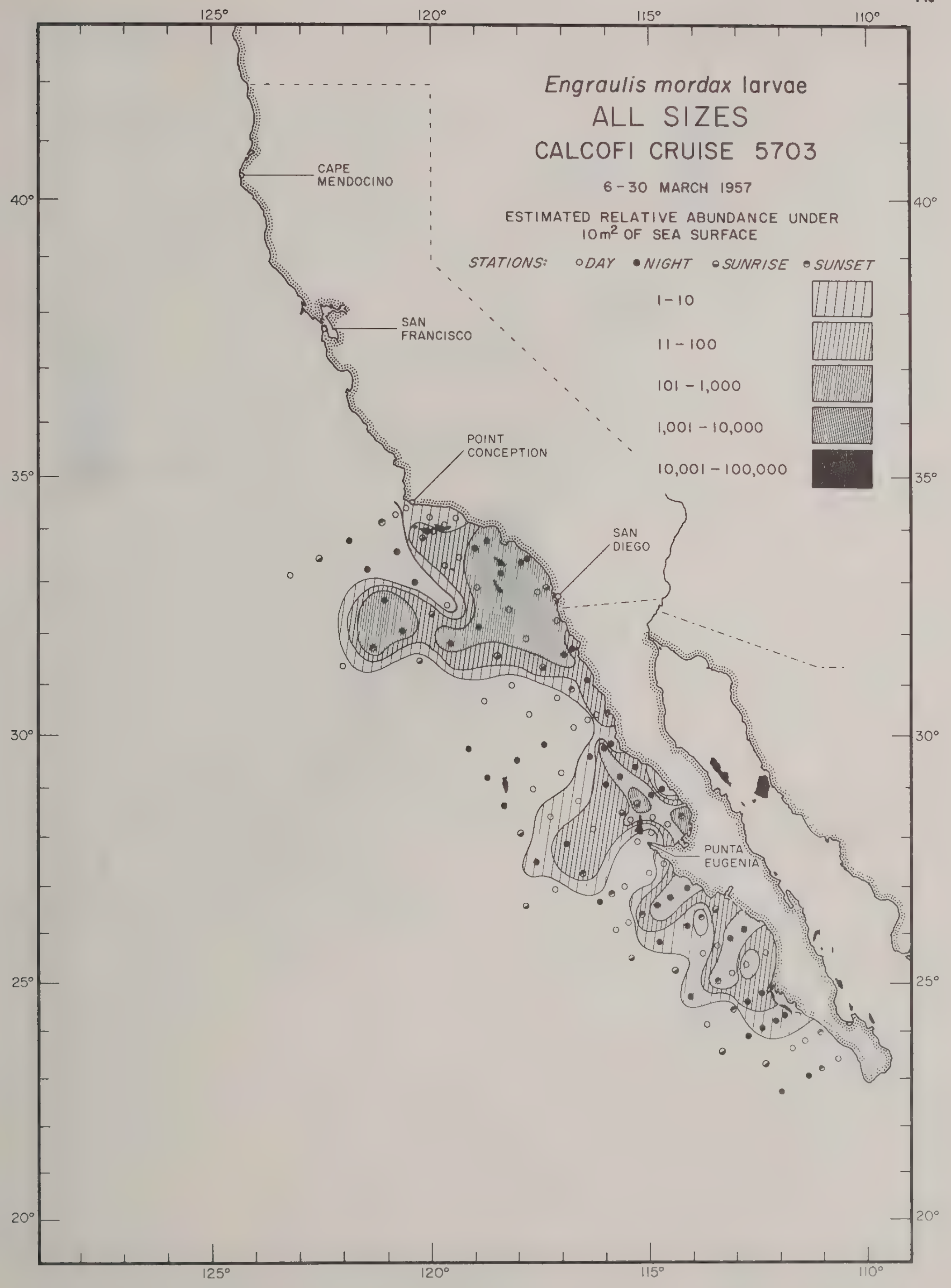
5702


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5703
6-30 MARCH 1957
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT SUNRISE SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

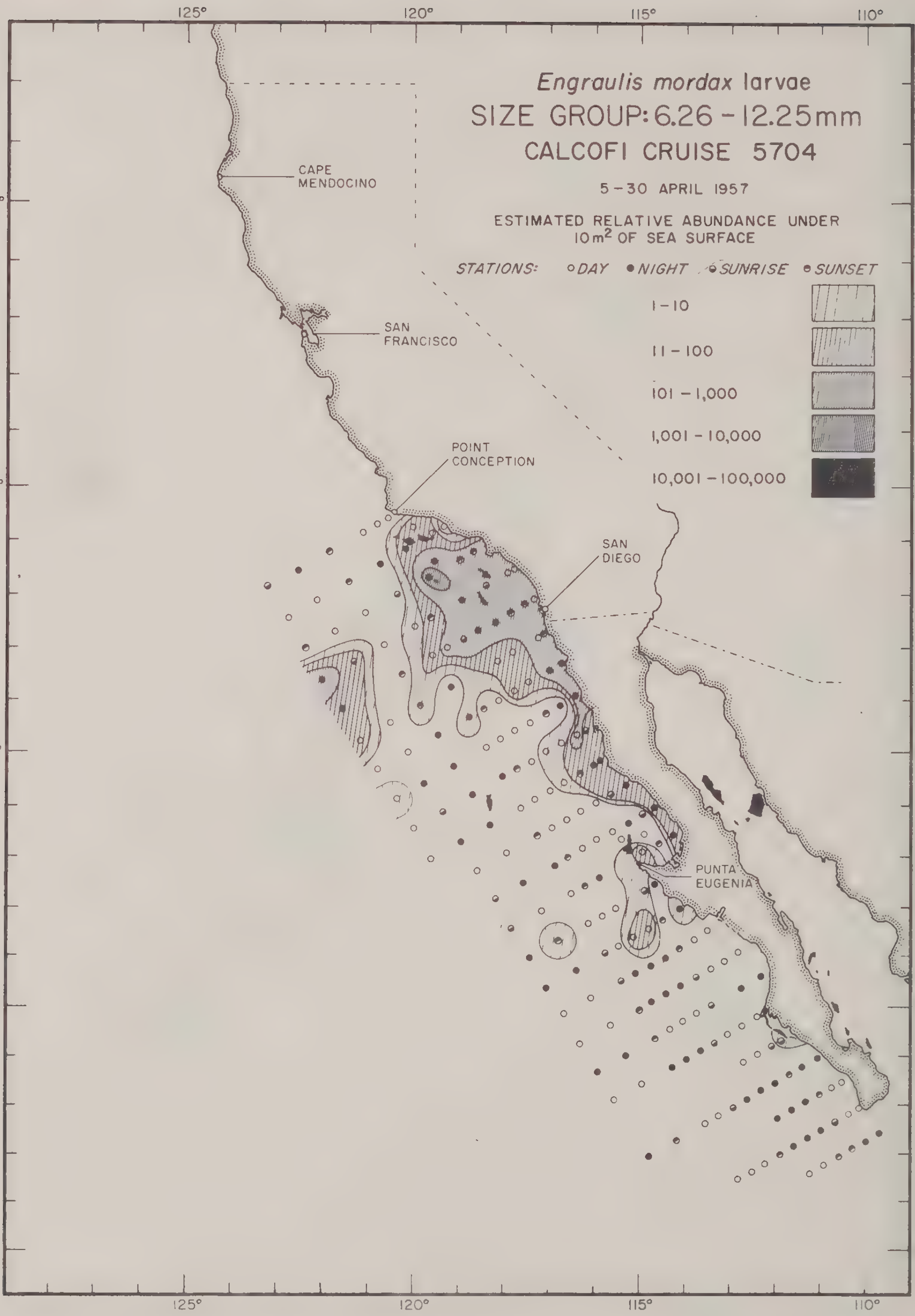
Size Group: 6.26-12.25mm

5703


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5703
6 - 30 MARCH 1957
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT SUNRISE SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

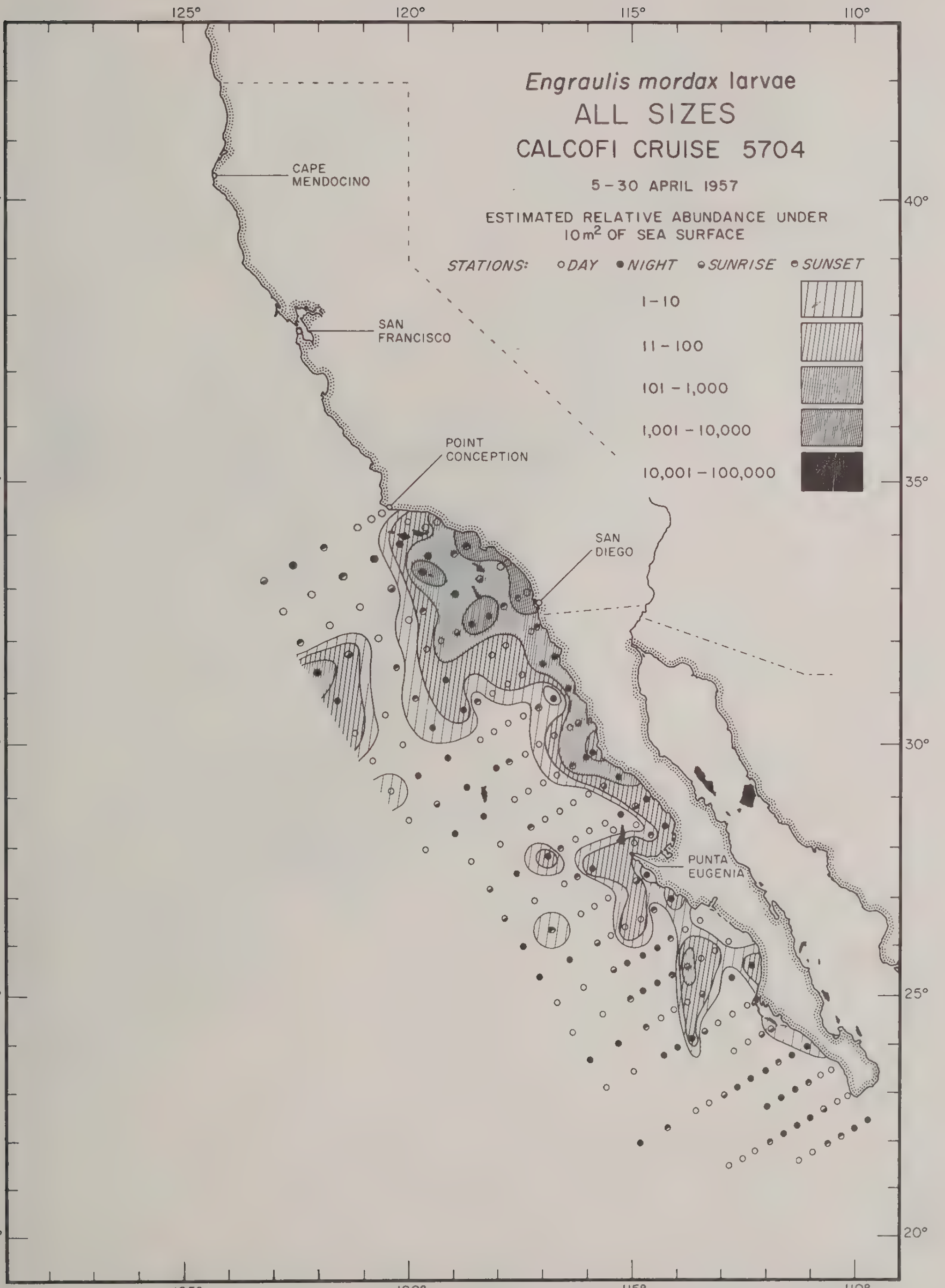
All Sizes
5703


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5704
5 - 30 APRIL 1957
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

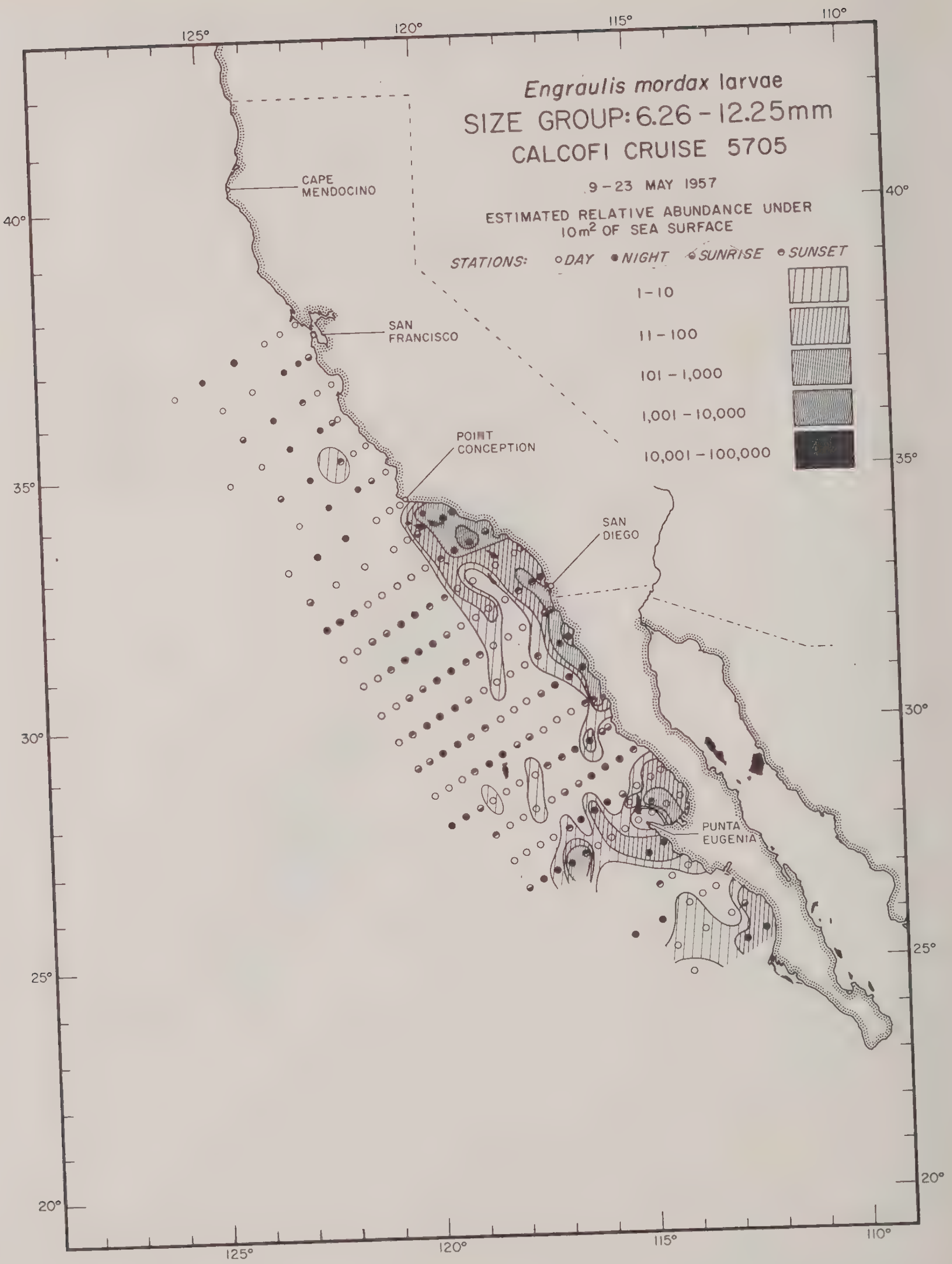
5704


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5704
5 – 30 APRIL 1957
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

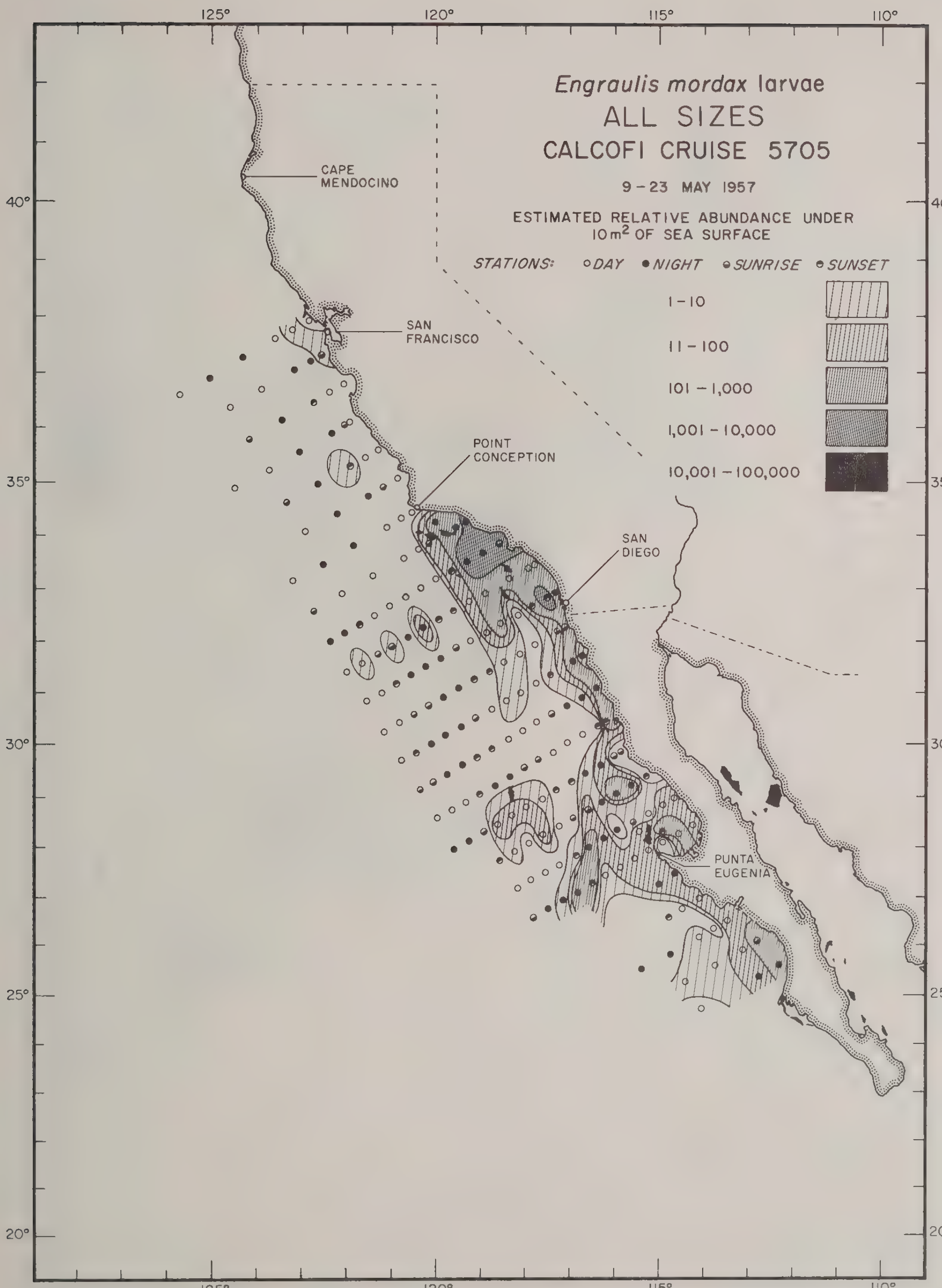
All Sizes

5704


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5705
9 - 23 MAY 1957
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT SUNRISE SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

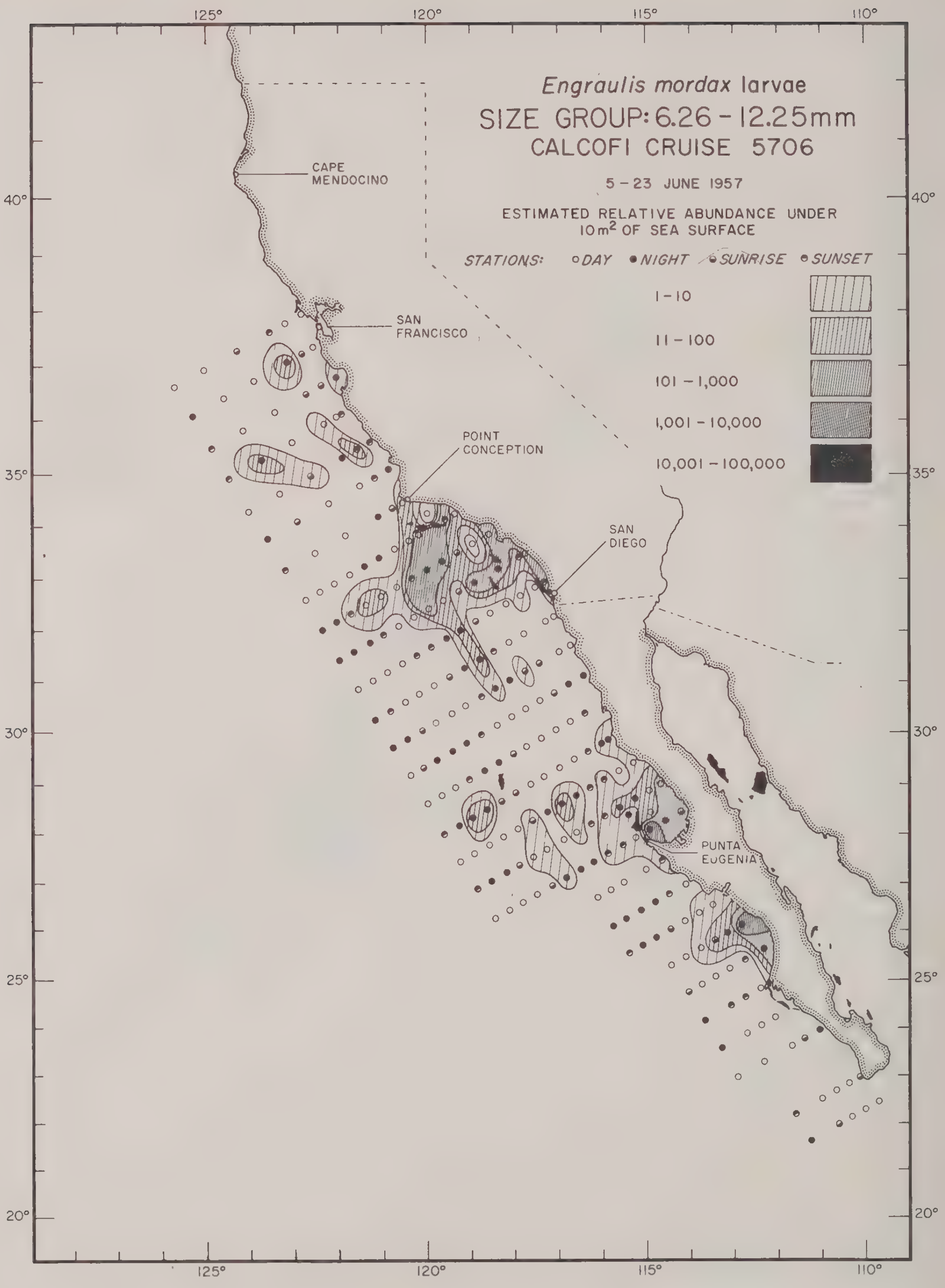
Size Group: 6.26-12.25mm
5705


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5705
9 – 23 MAY 1957
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

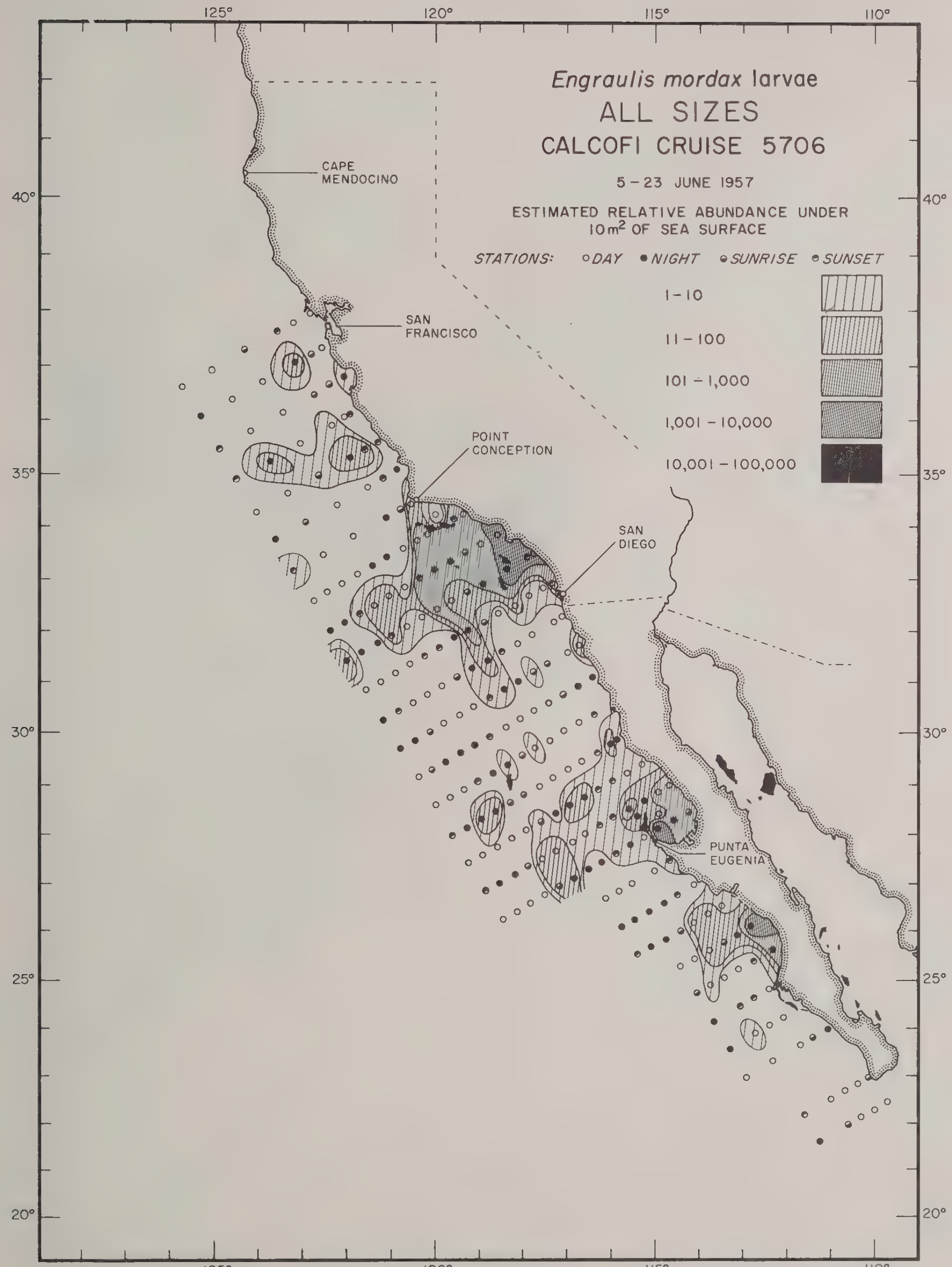
5705


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5706
5 - 23 JUNE 1957
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

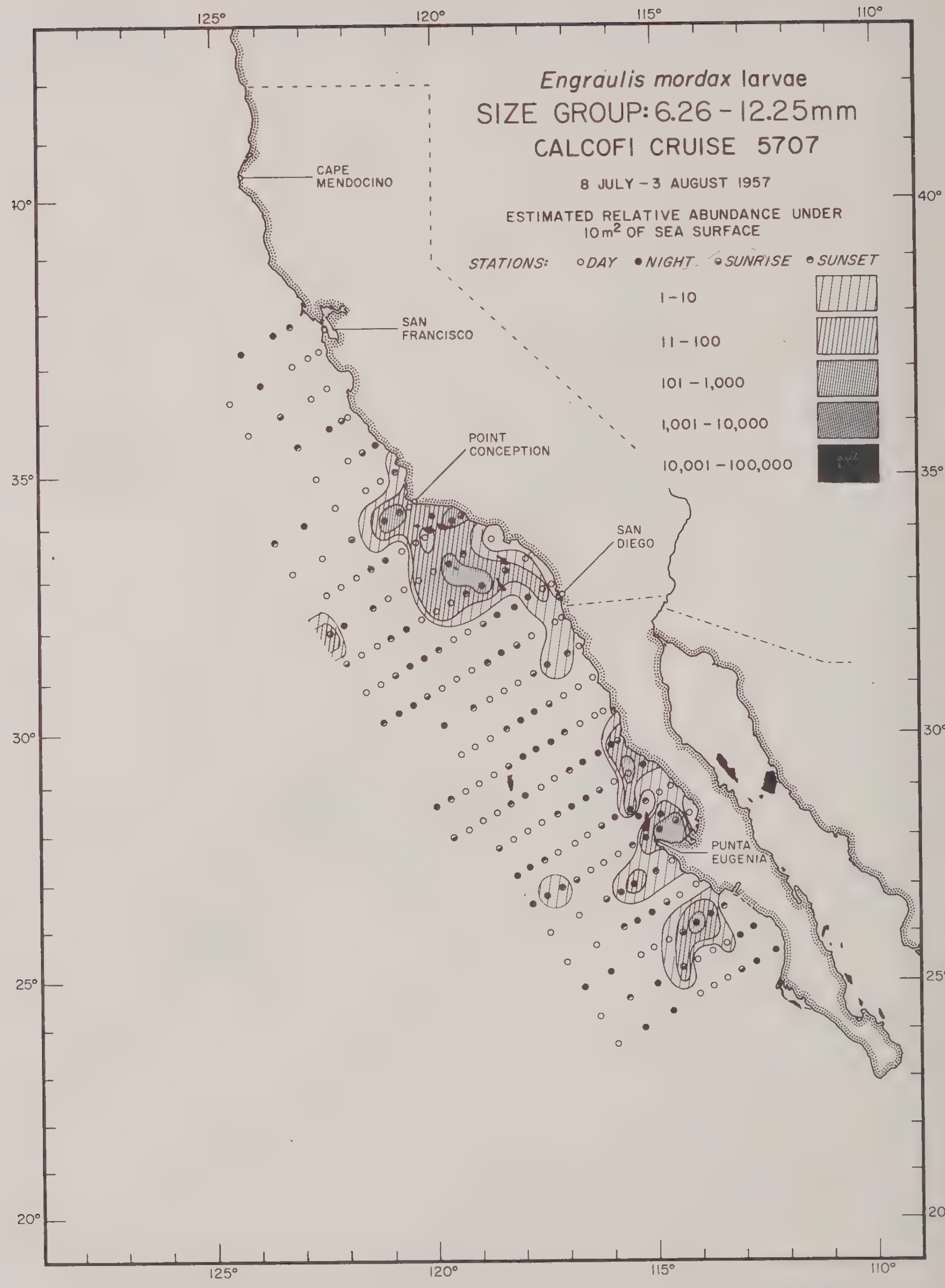
5706


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5706
5 – 23 JUNE 1957
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

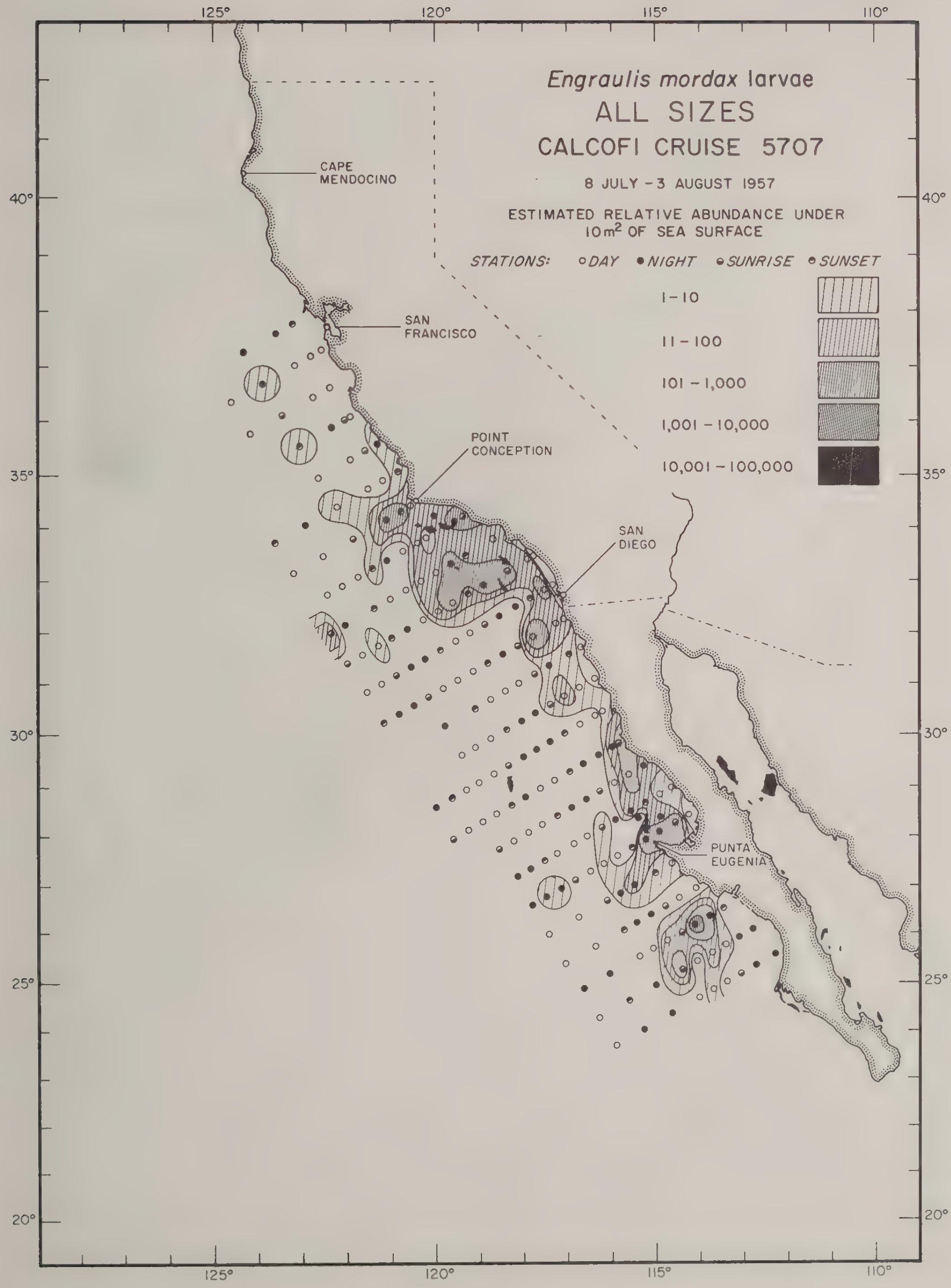
5706


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5707
8 JULY - 3 AUGUST 1957
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◉ SUNRISE ◉ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

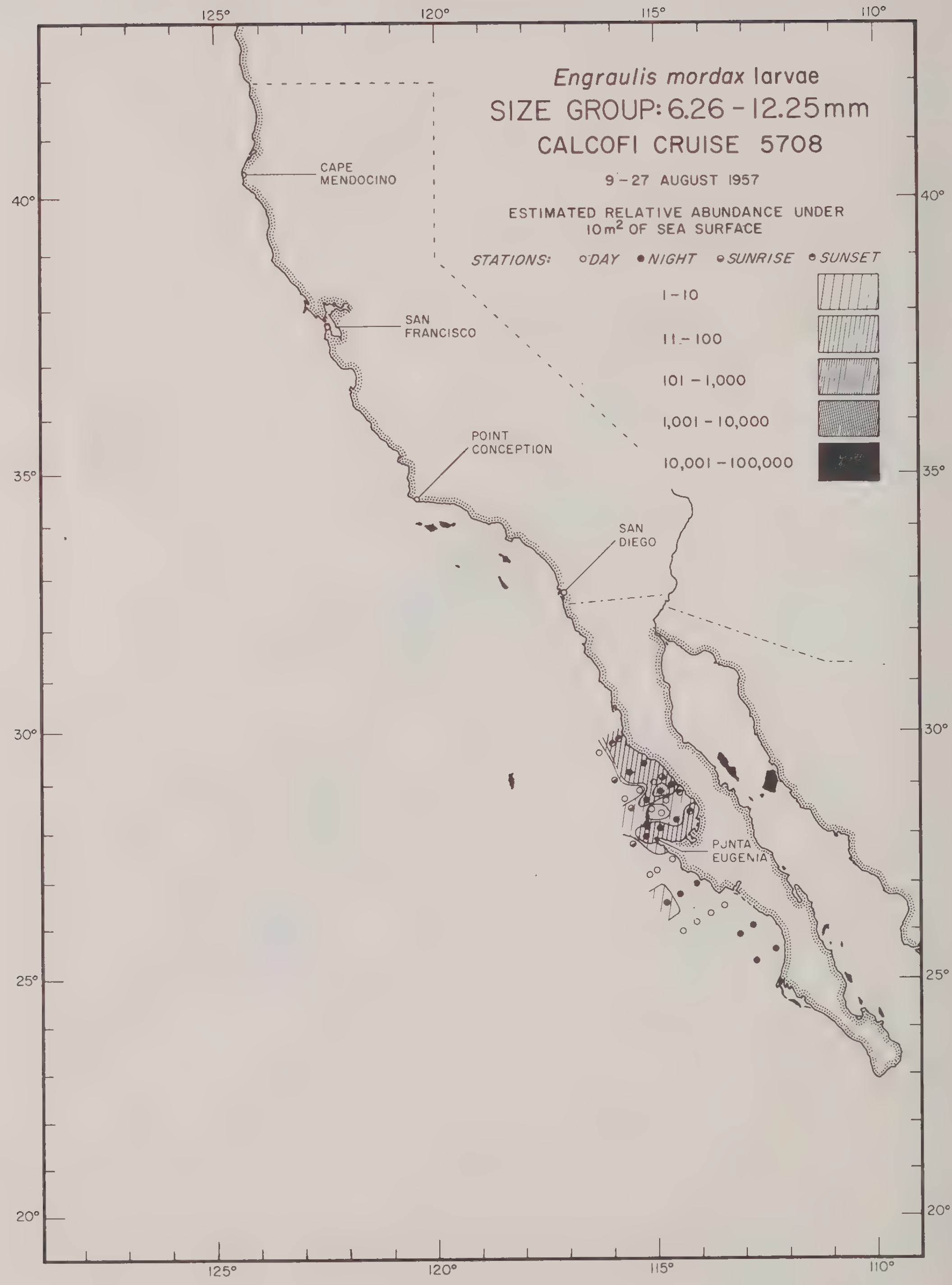
5707


125°
120°
115°
110°
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5707
8 JULY – 3 AUGUST 1957
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

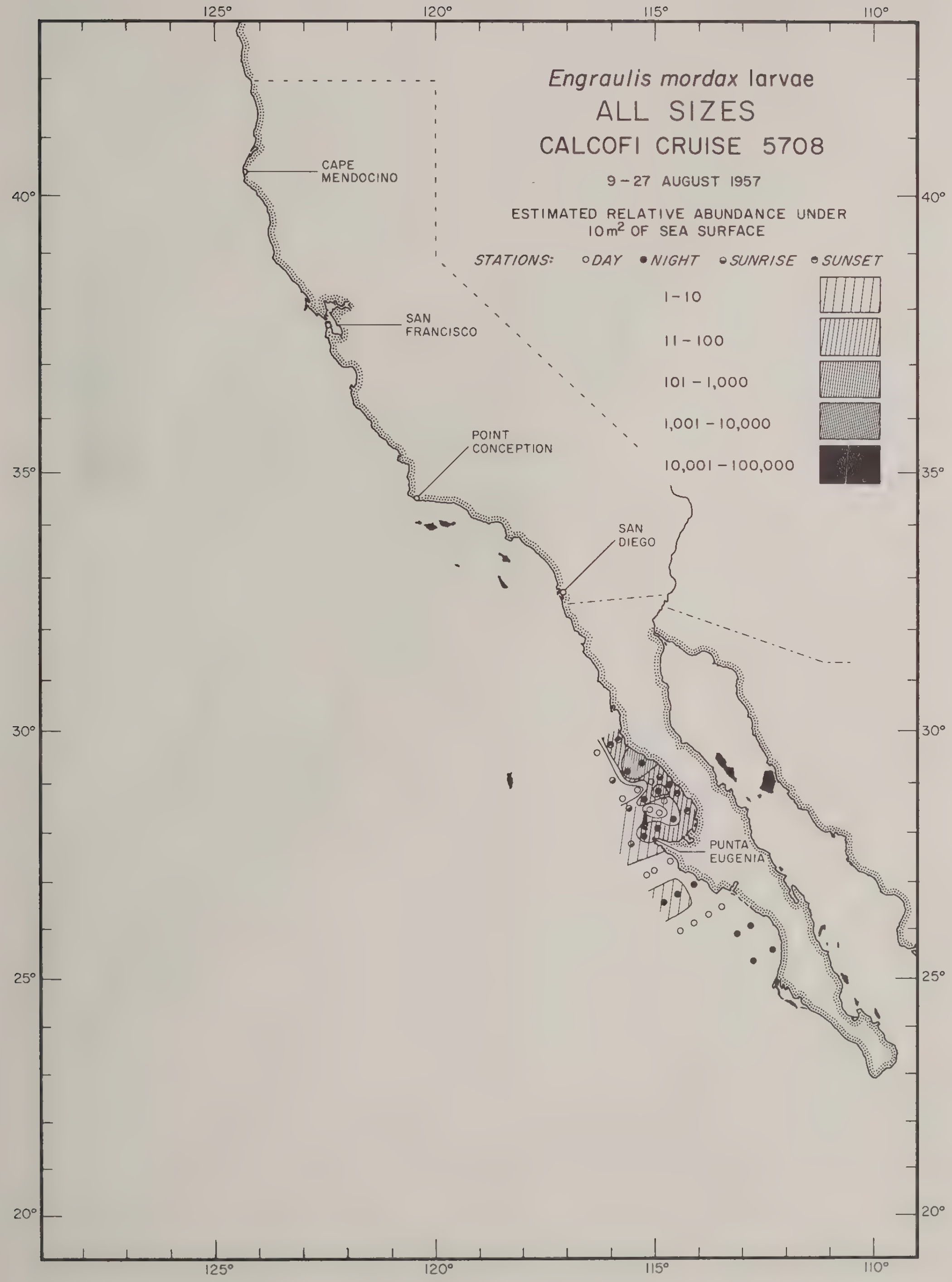
5707


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5708
9 - 27 AUGUST 1957
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◉ SUNRISE ◉ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

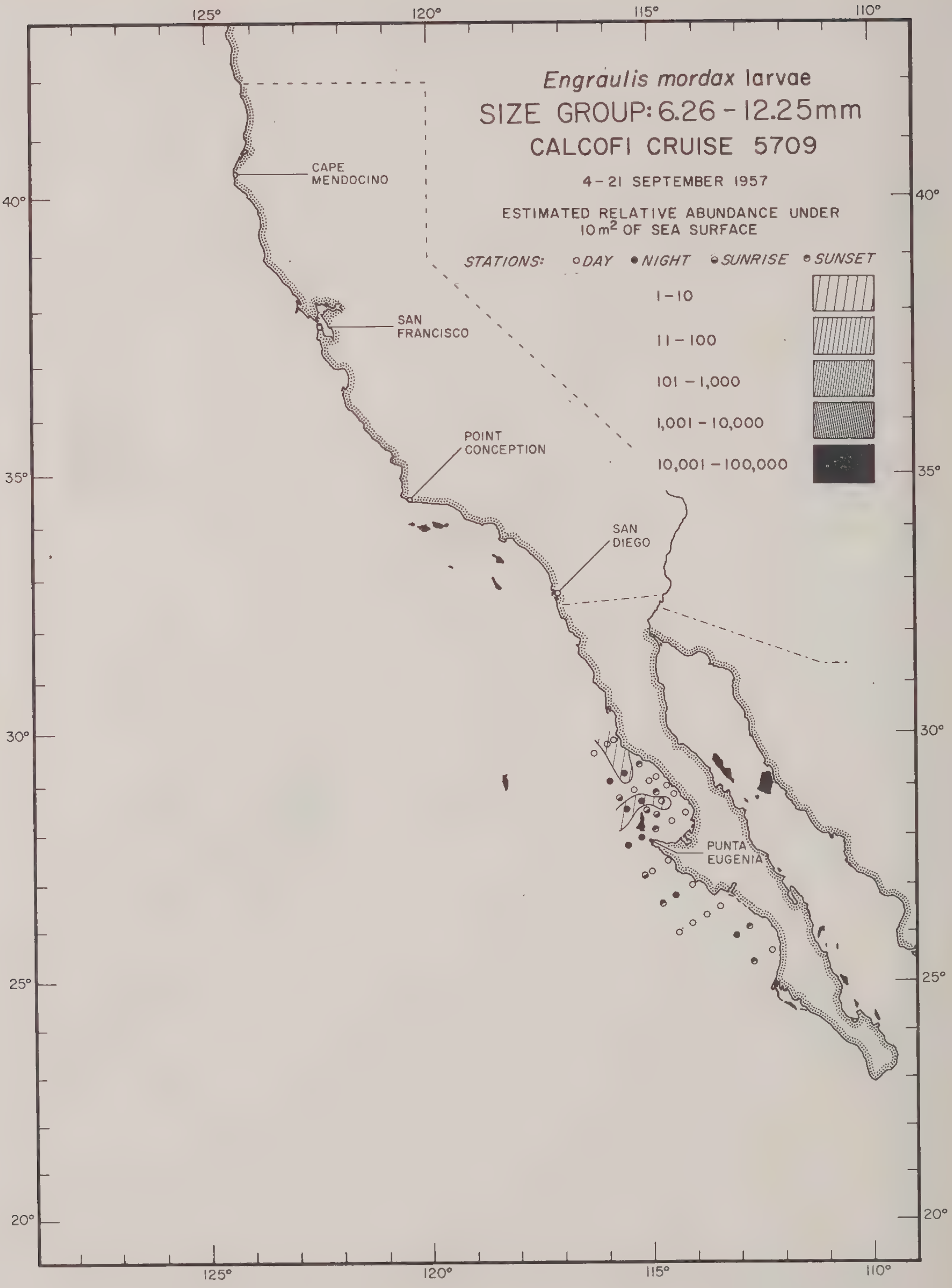
5708


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5708
9 - 27 AUGUST 1957
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

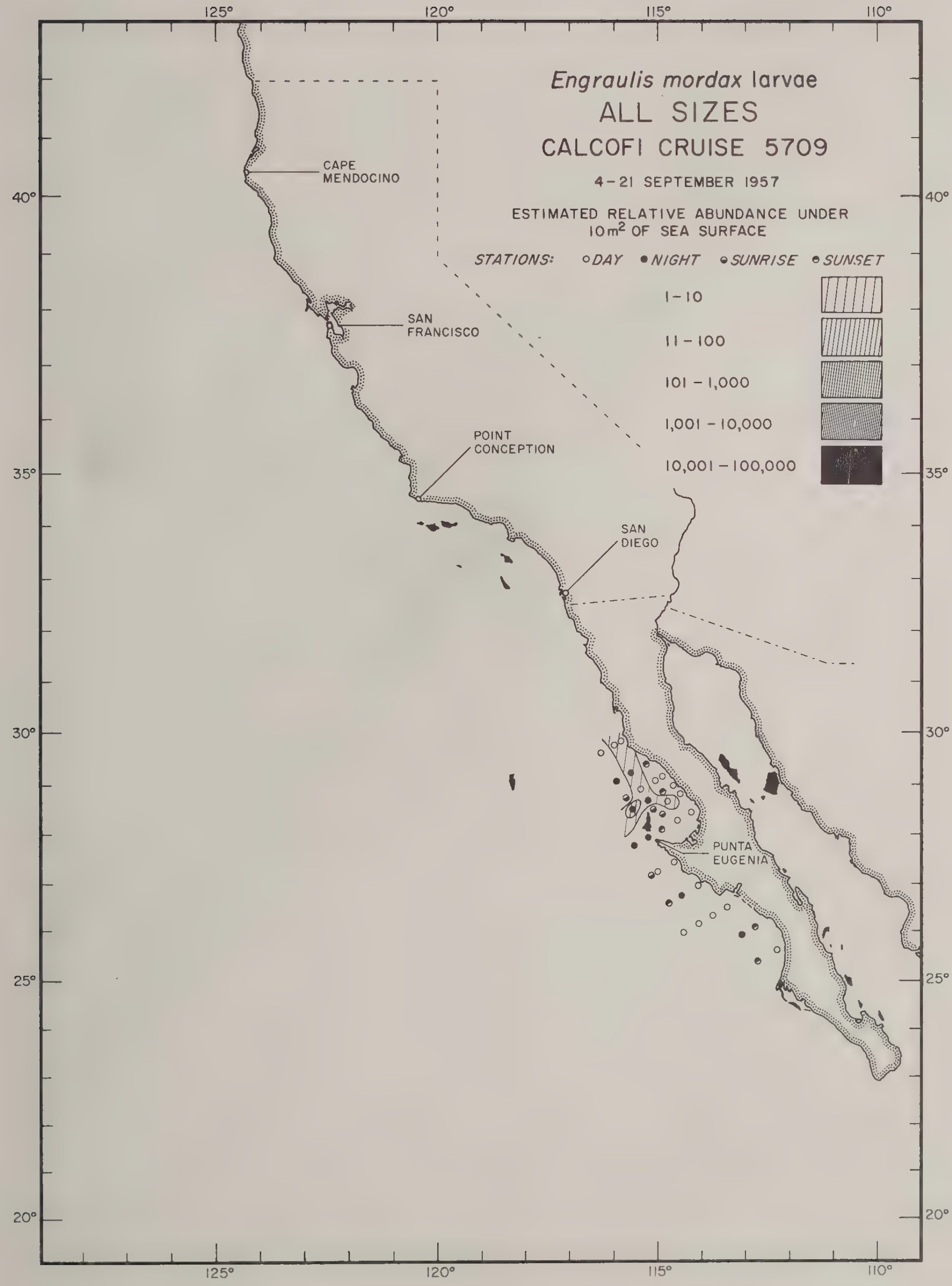
5708


125°
120°
115°
110°
Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5709
4 - 21 SEPTEMBER 1957
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
40°
35°
30°
25°
20°

Engraulis mordax larvae

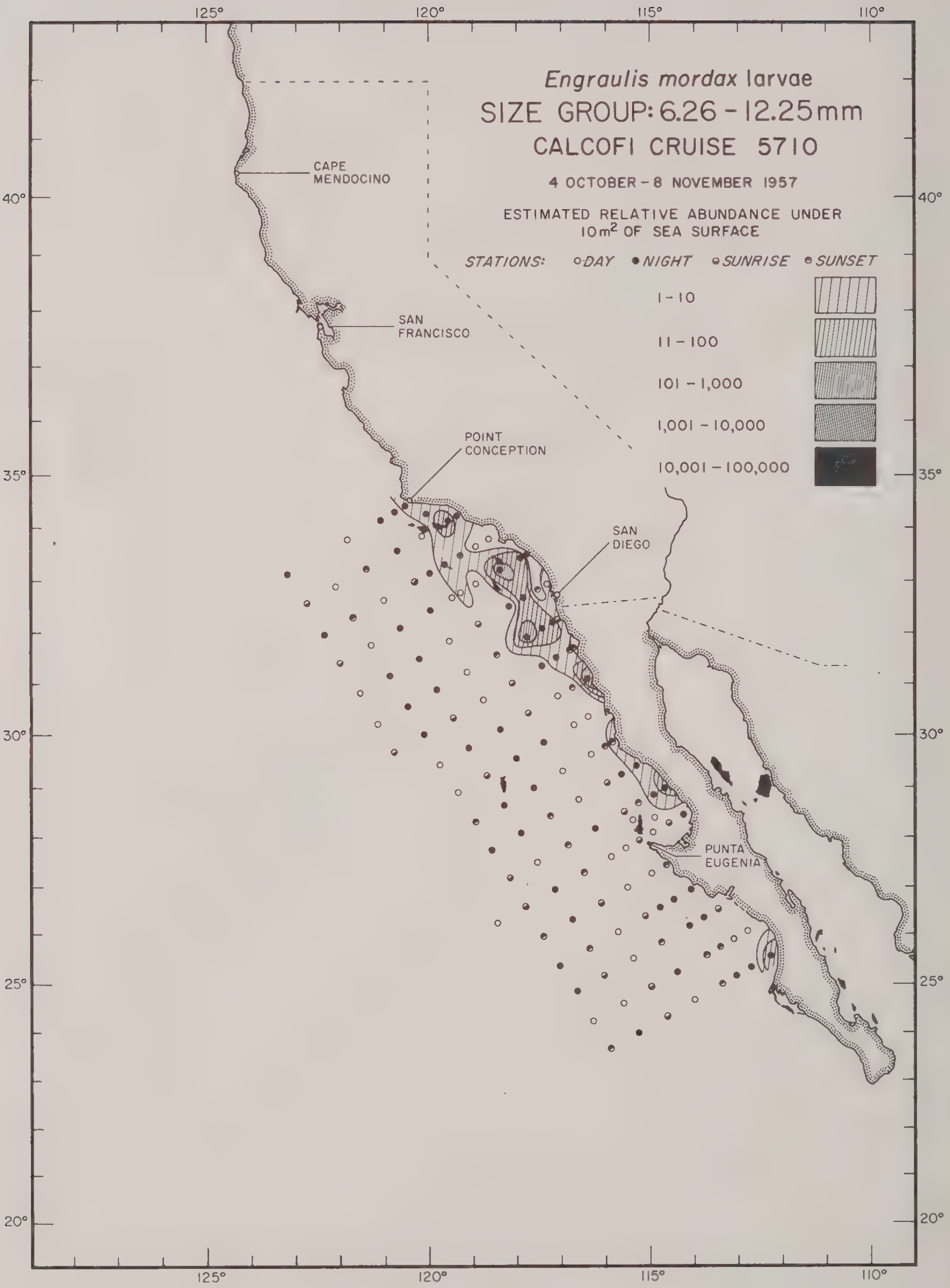
Size Group: 6.26-12.25mm

5709


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5709
4-21 SEPTEMBER 1957
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

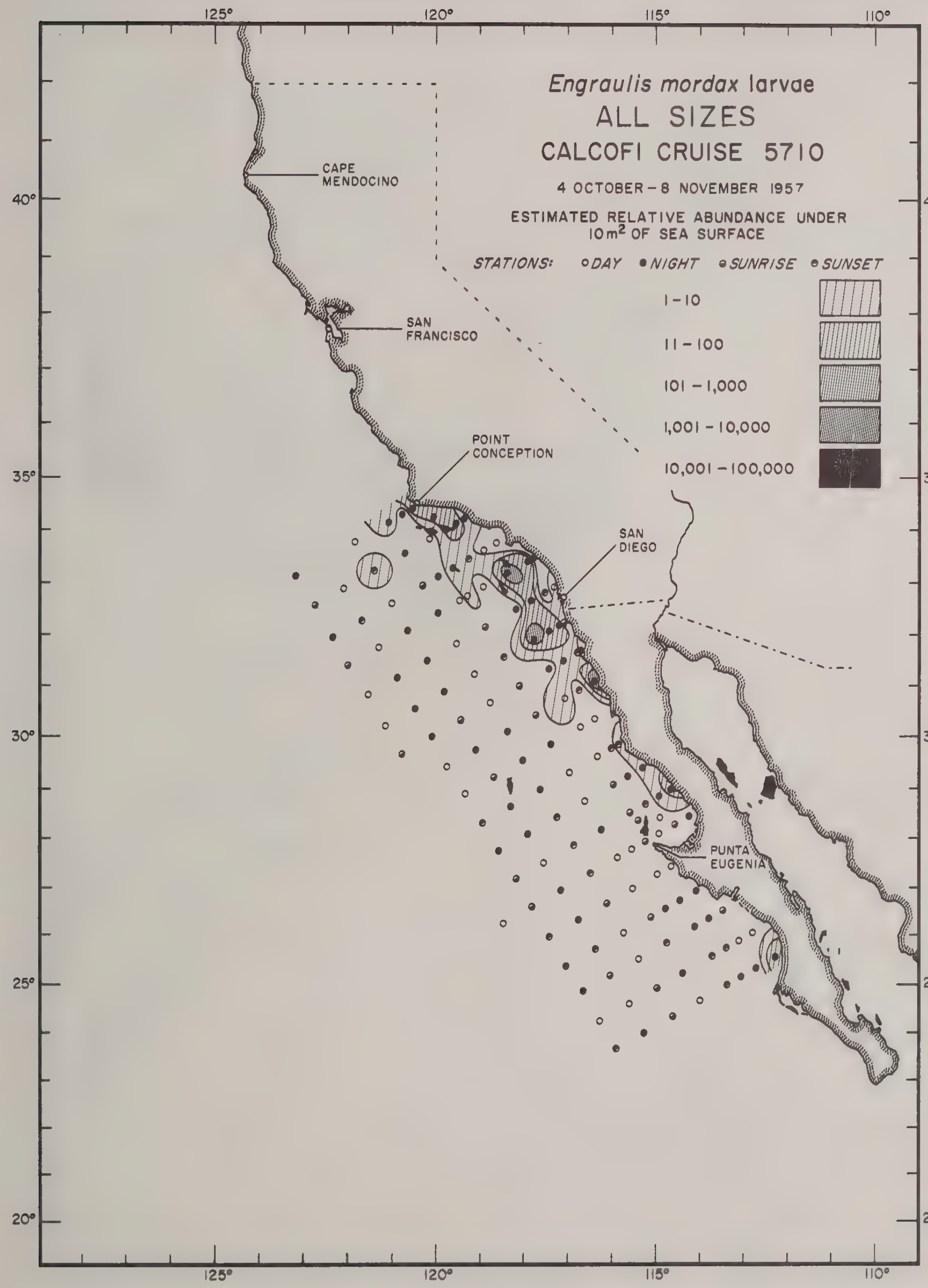
All Sizes
5709


125°
120°
115°
110°
Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5710
4 OCTOBER - 8 NOVEMBER 1957
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

5710

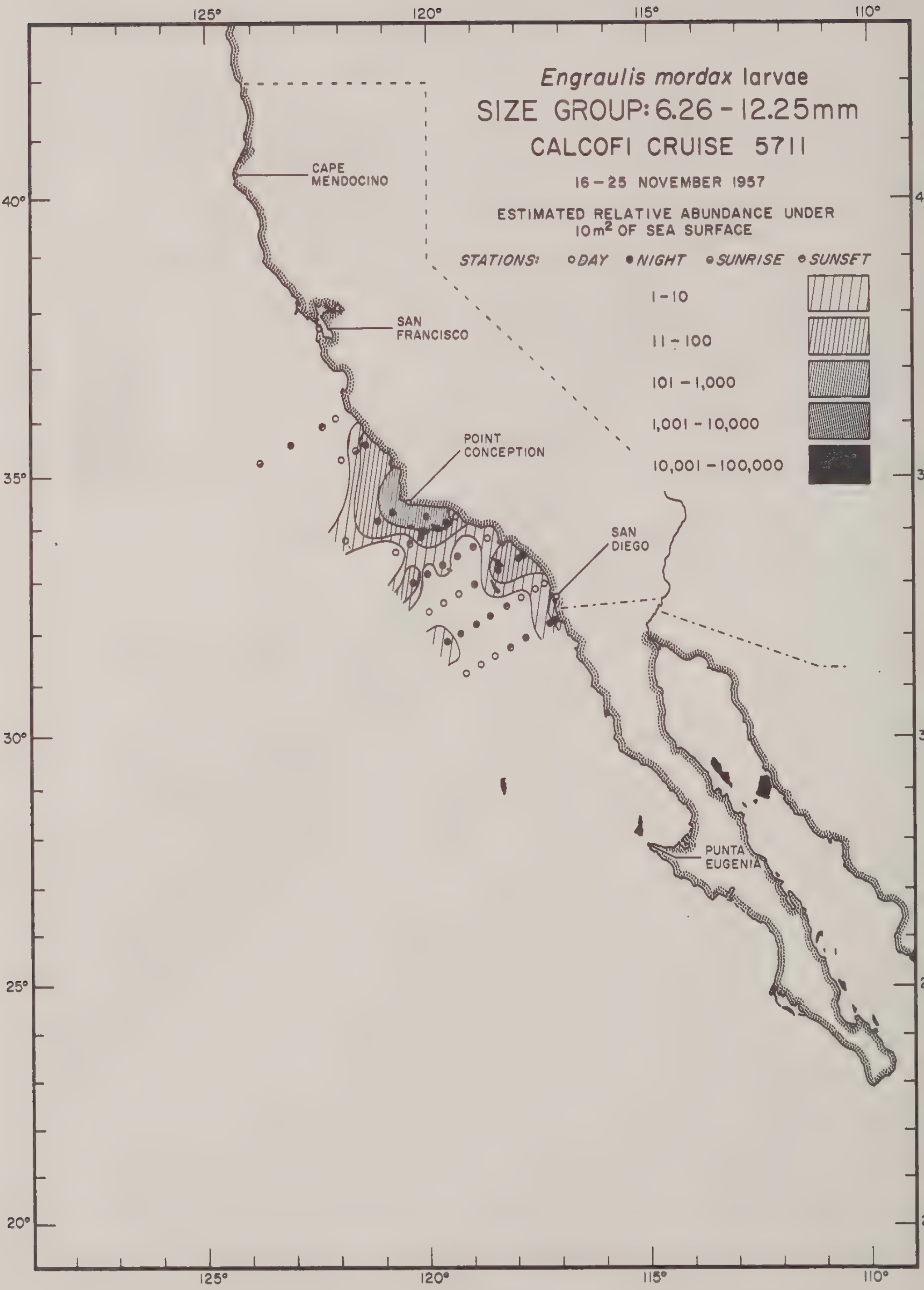


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5710
4 OCTOBER – 8 NOVEMBER 1957
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ● SUNRISE ● SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

All Sizes

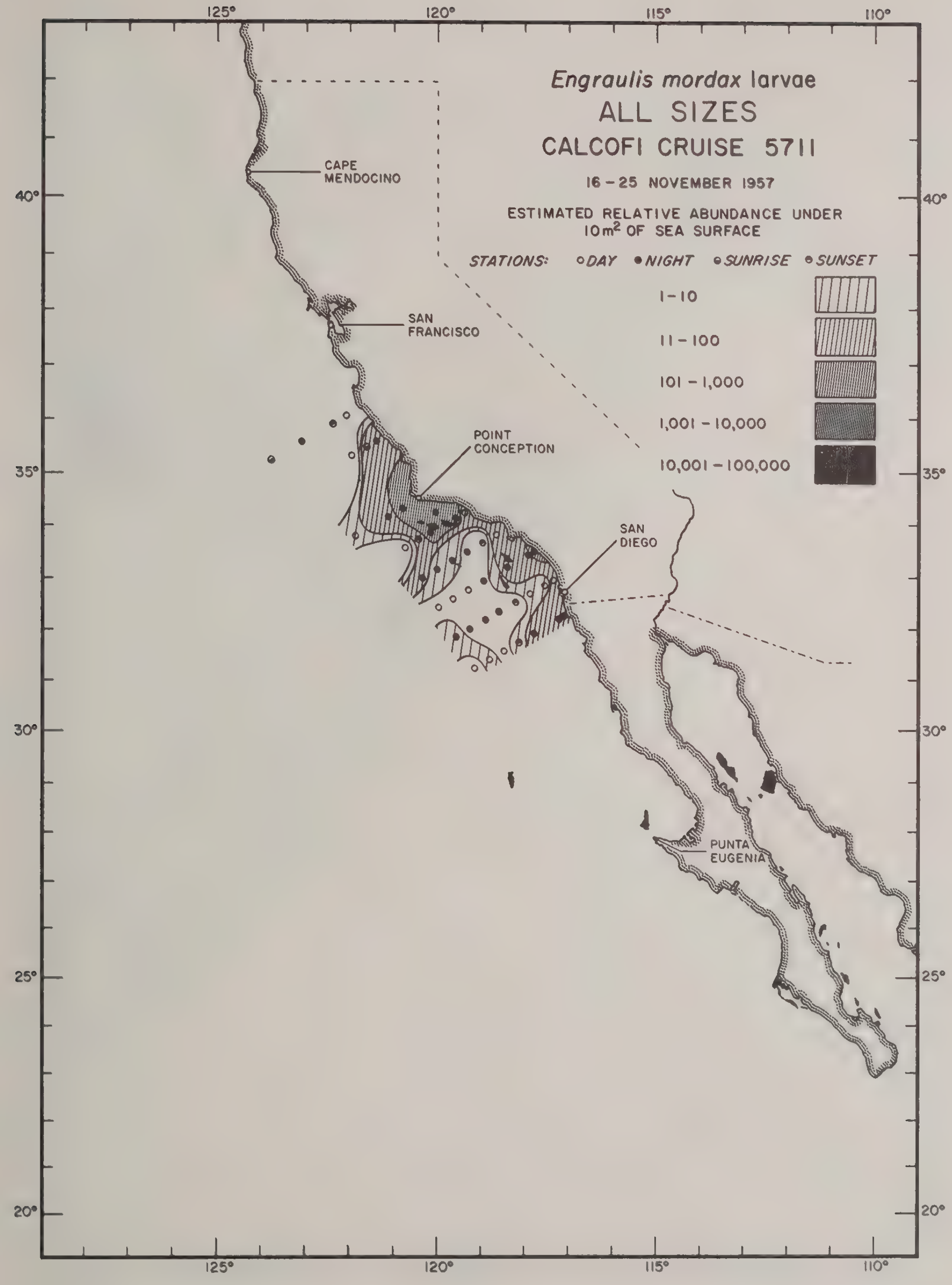
5710


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5711
16 – 25 NOVEMBER 1957
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◉ SUNRISE ◉ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

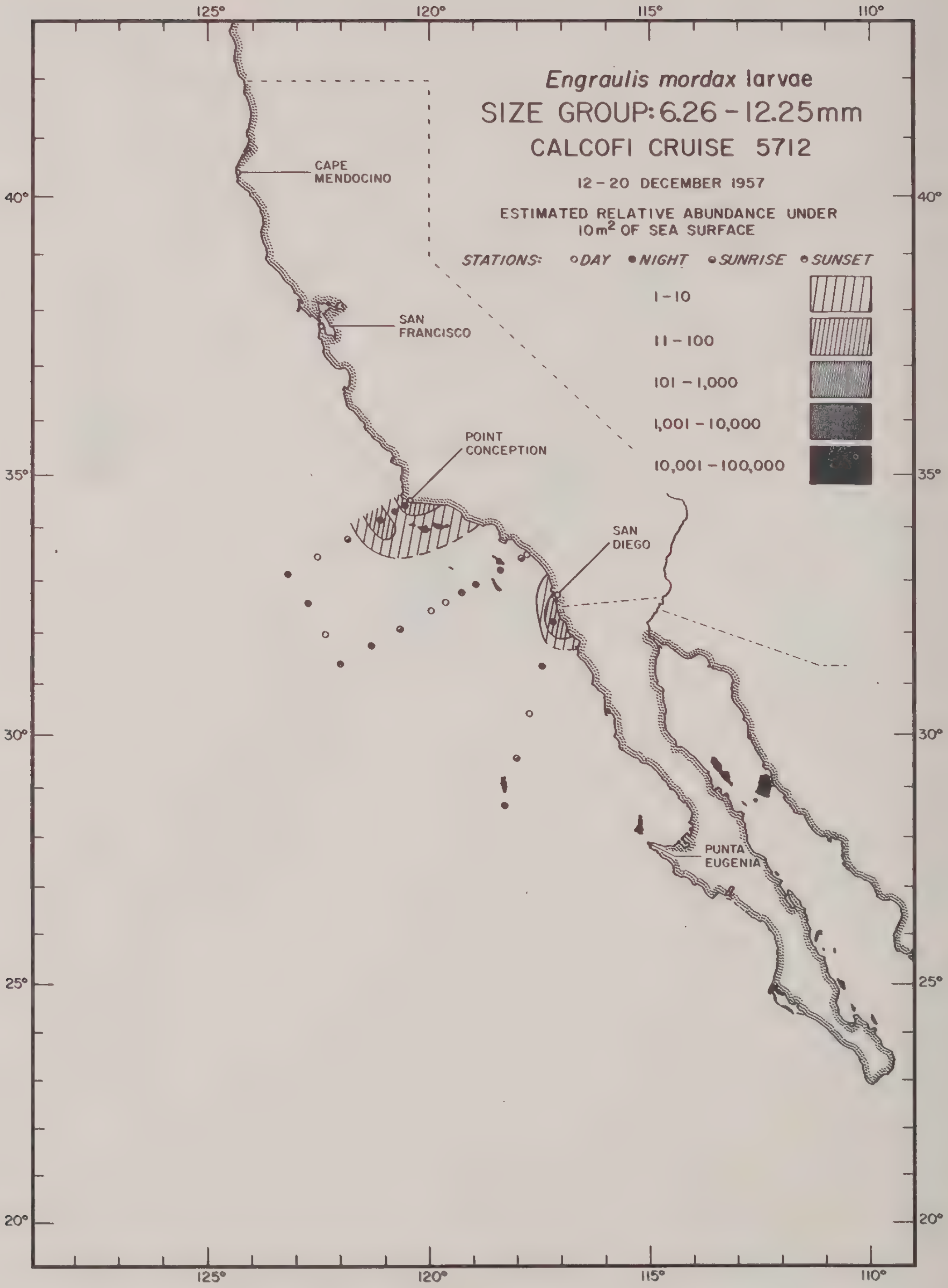
5711


125°
120°
115°
110°
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5711
16 - 25 NOVEMBER 1957
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◉ SUNRISE ◉ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

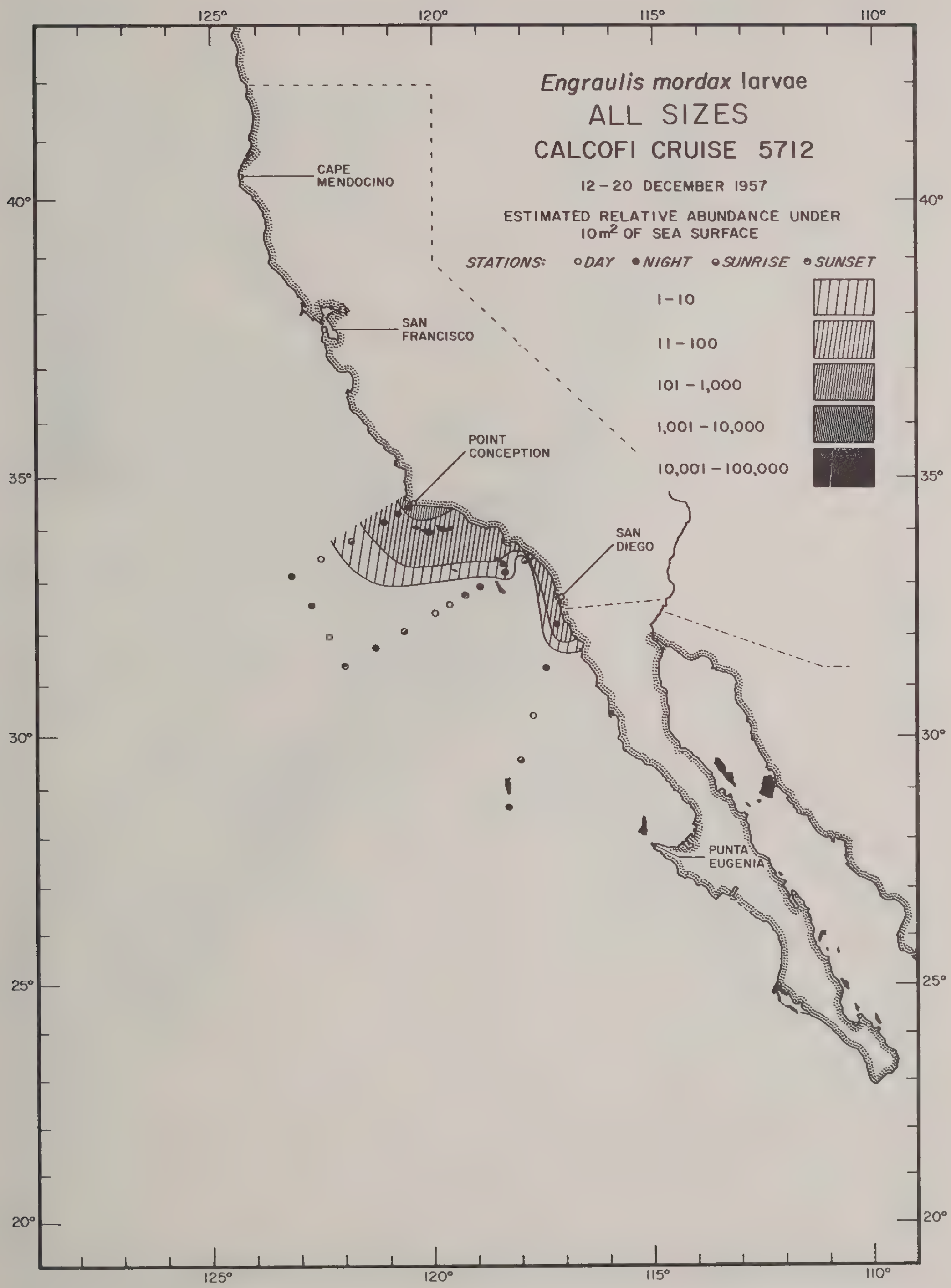
5711


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5712
12 - 20 DECEMBER 1957
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◉ SUNRISE ◉ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

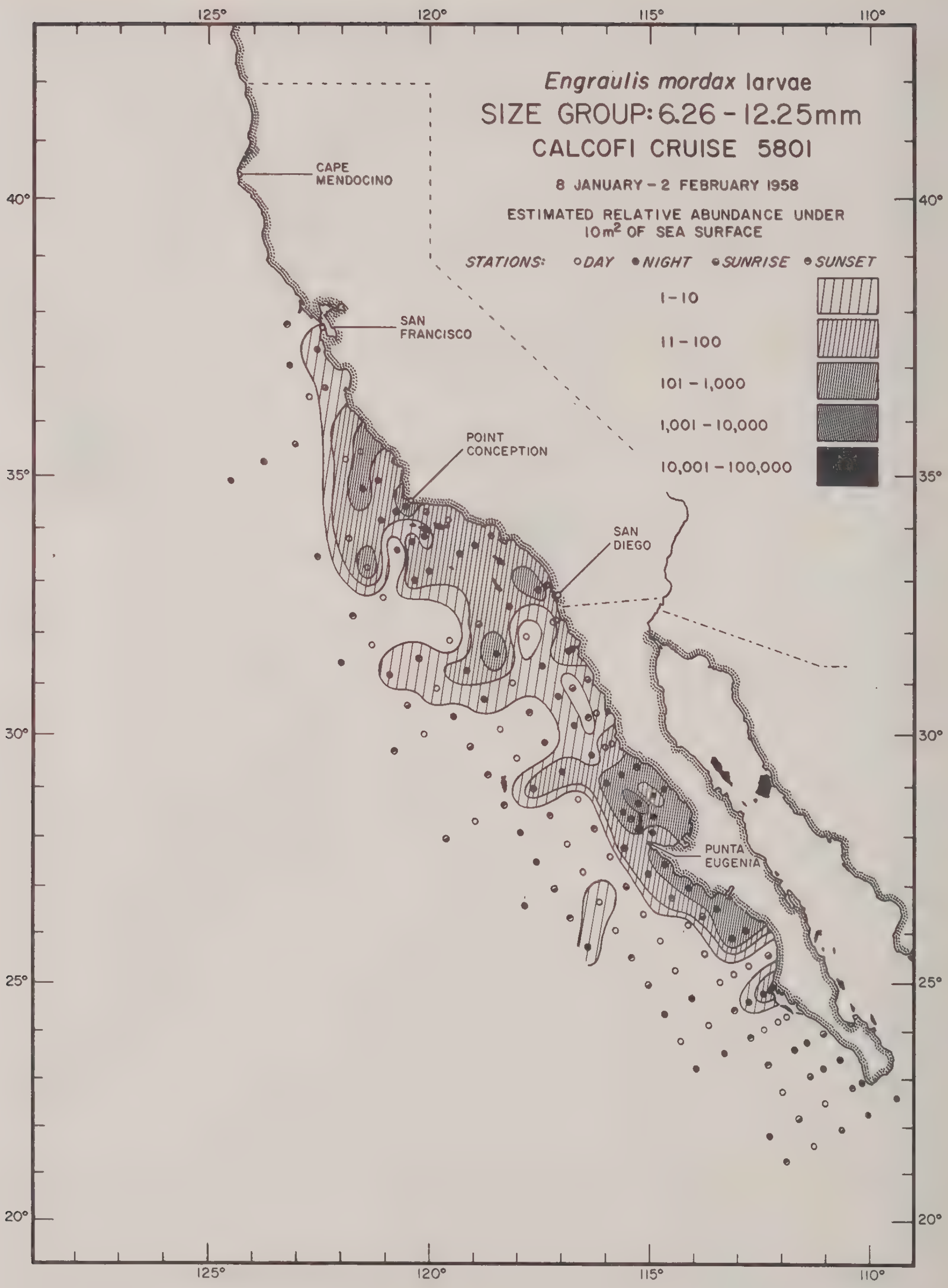
5712


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5712
12 – 20 DECEMBER 1957
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

All Sizes

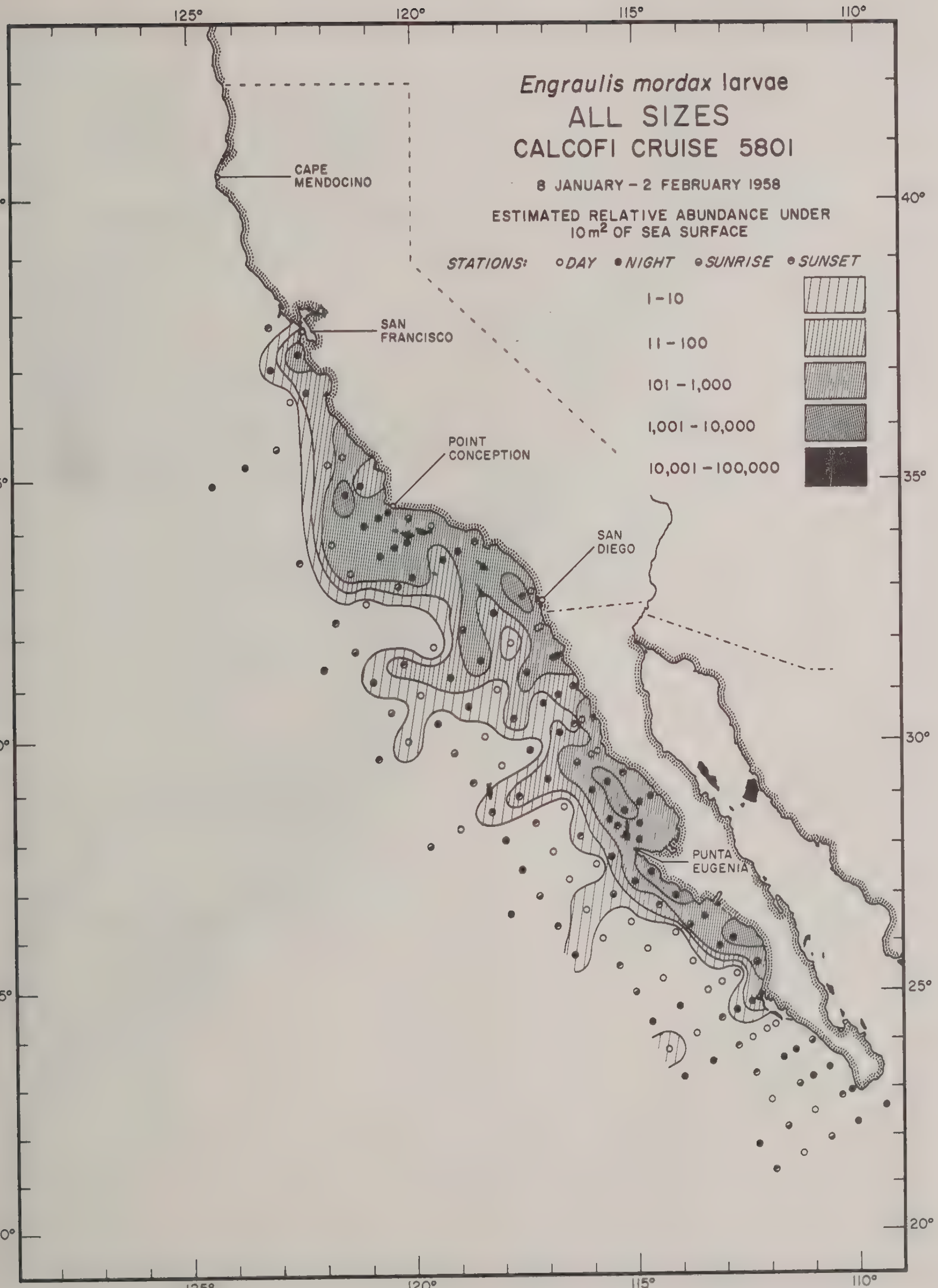
5712


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5801
8 JANUARY - 2 FEBRUARY 1958
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ● SUNRISE ● SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

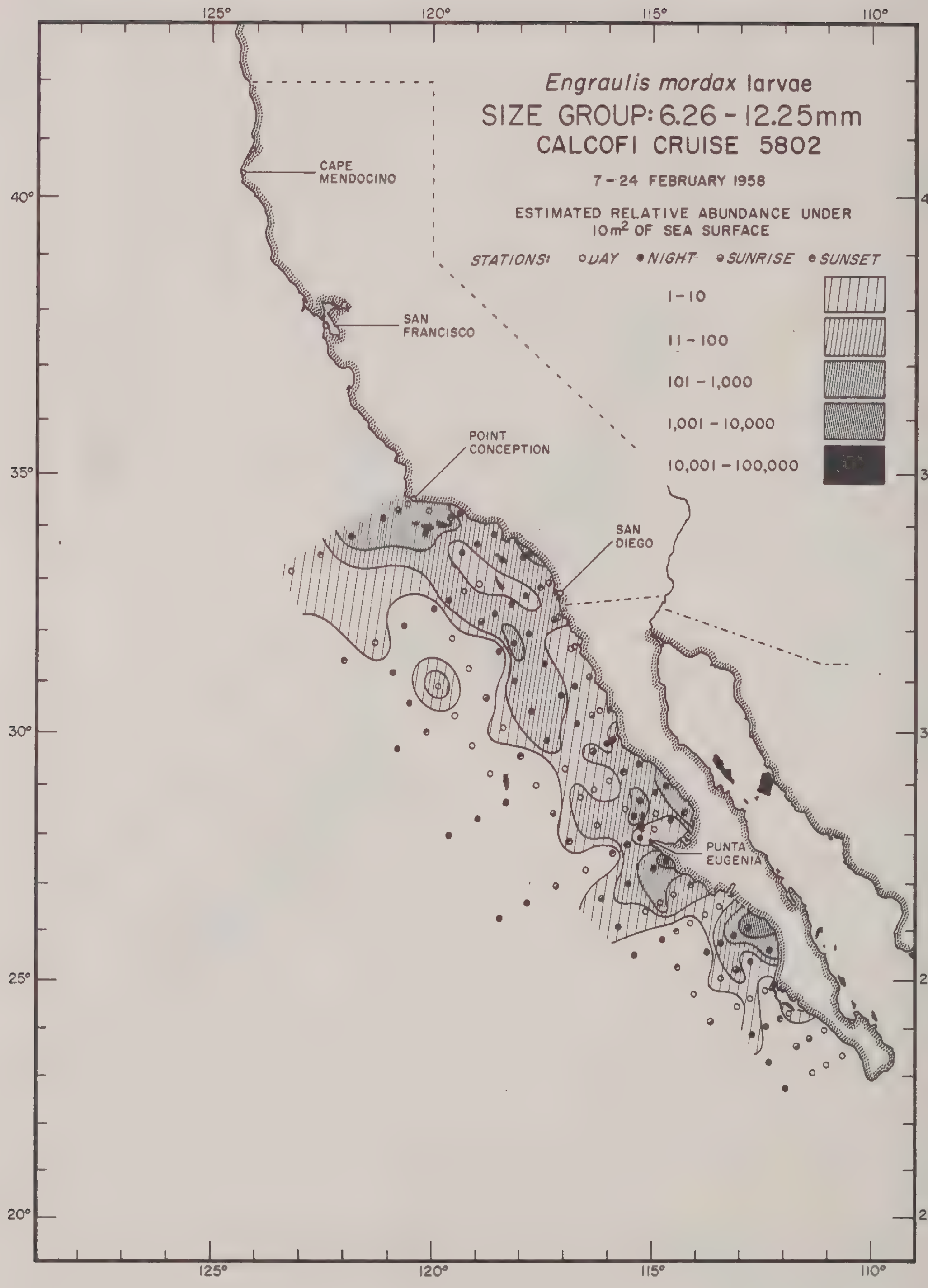
5801


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5801
8 JANUARY – 2 FEBRUARY 1958
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ● SUNRISE ● SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

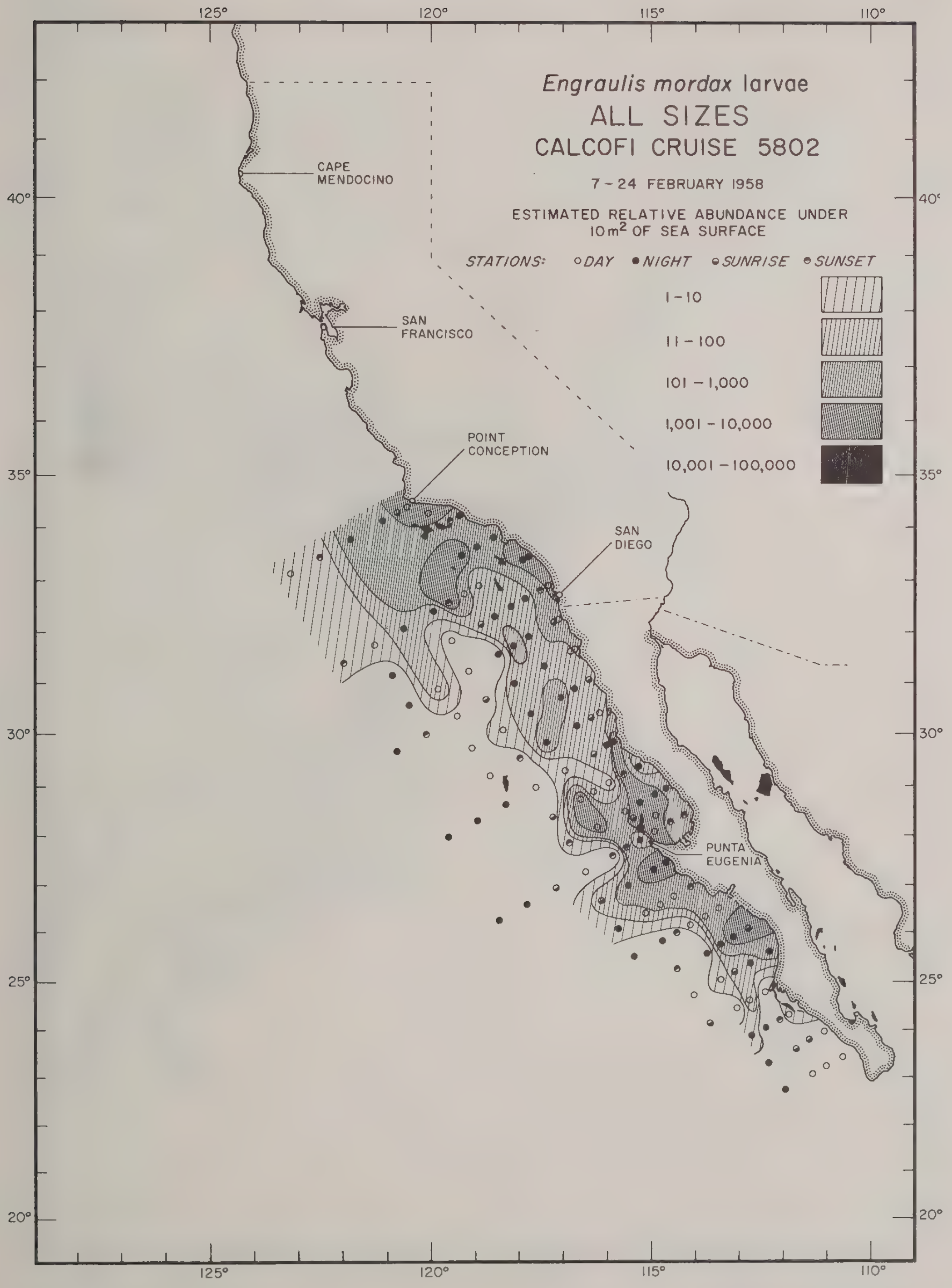
5801


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5802
7 - 24 FEBRUARY 1958
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

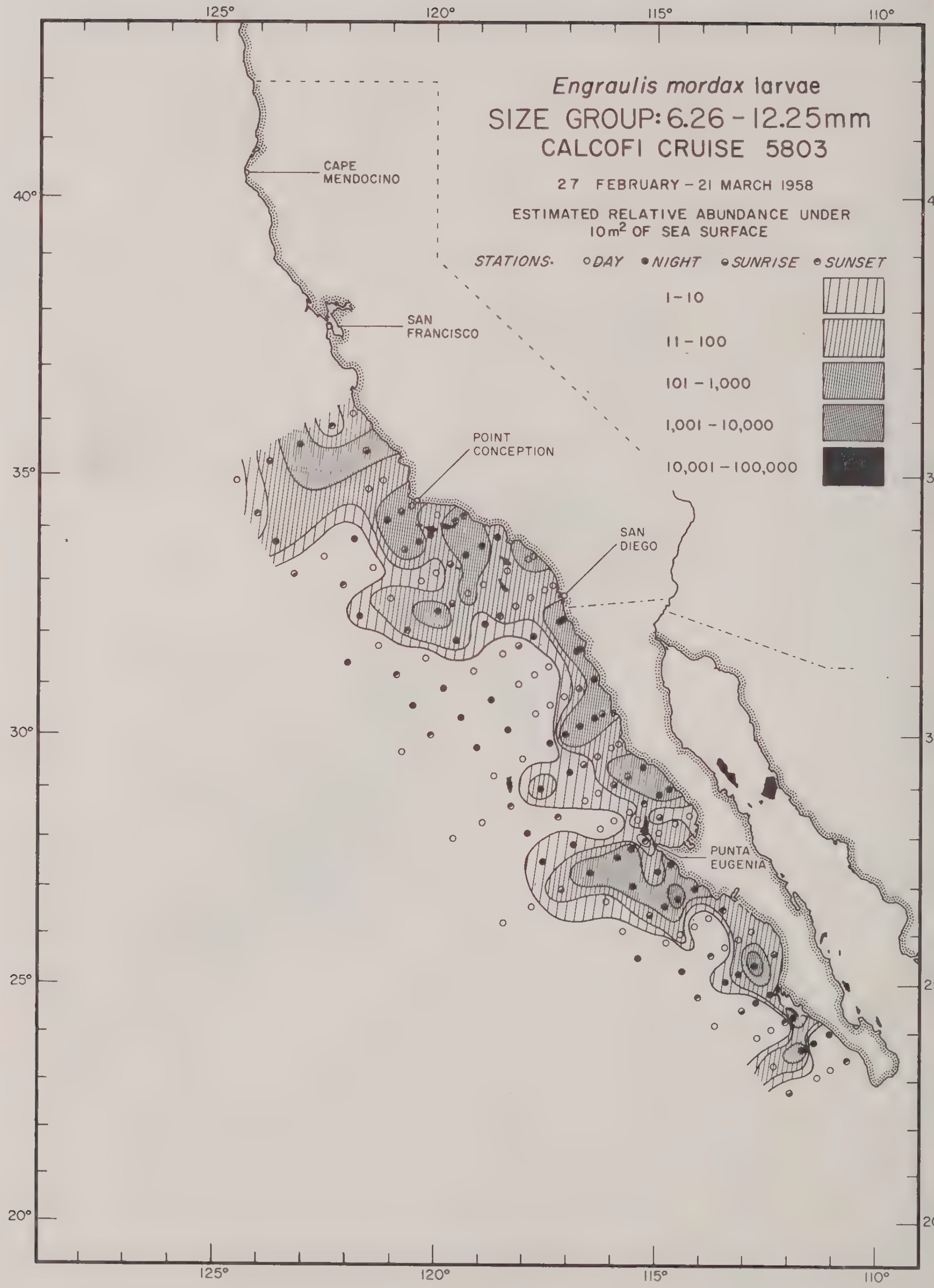
5802


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5802
7 – 24 FEBRUARY 1958
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

All Sizes

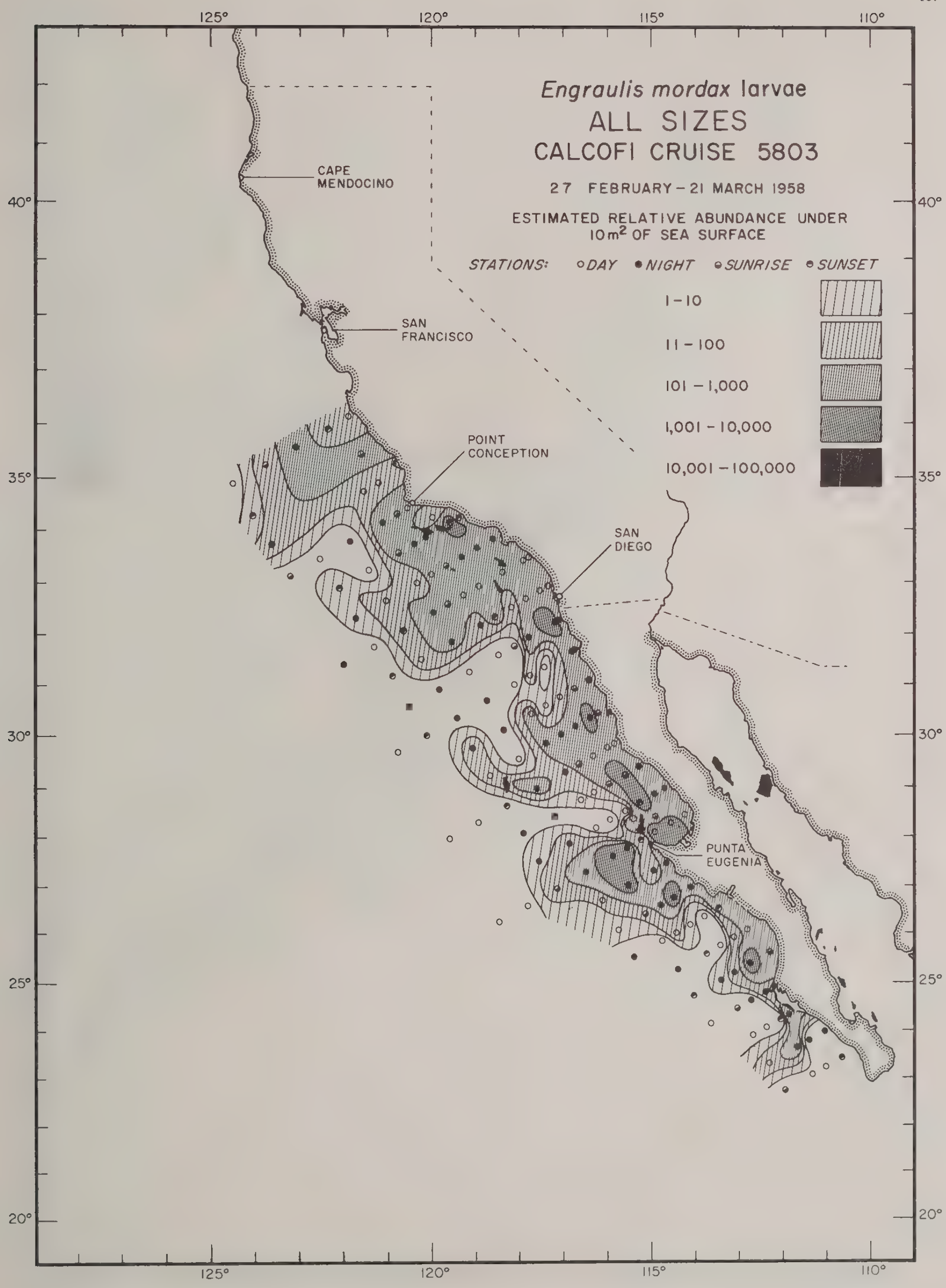
5802


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5803
27 FEBRUARY - 21 MARCH 1958
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

5803

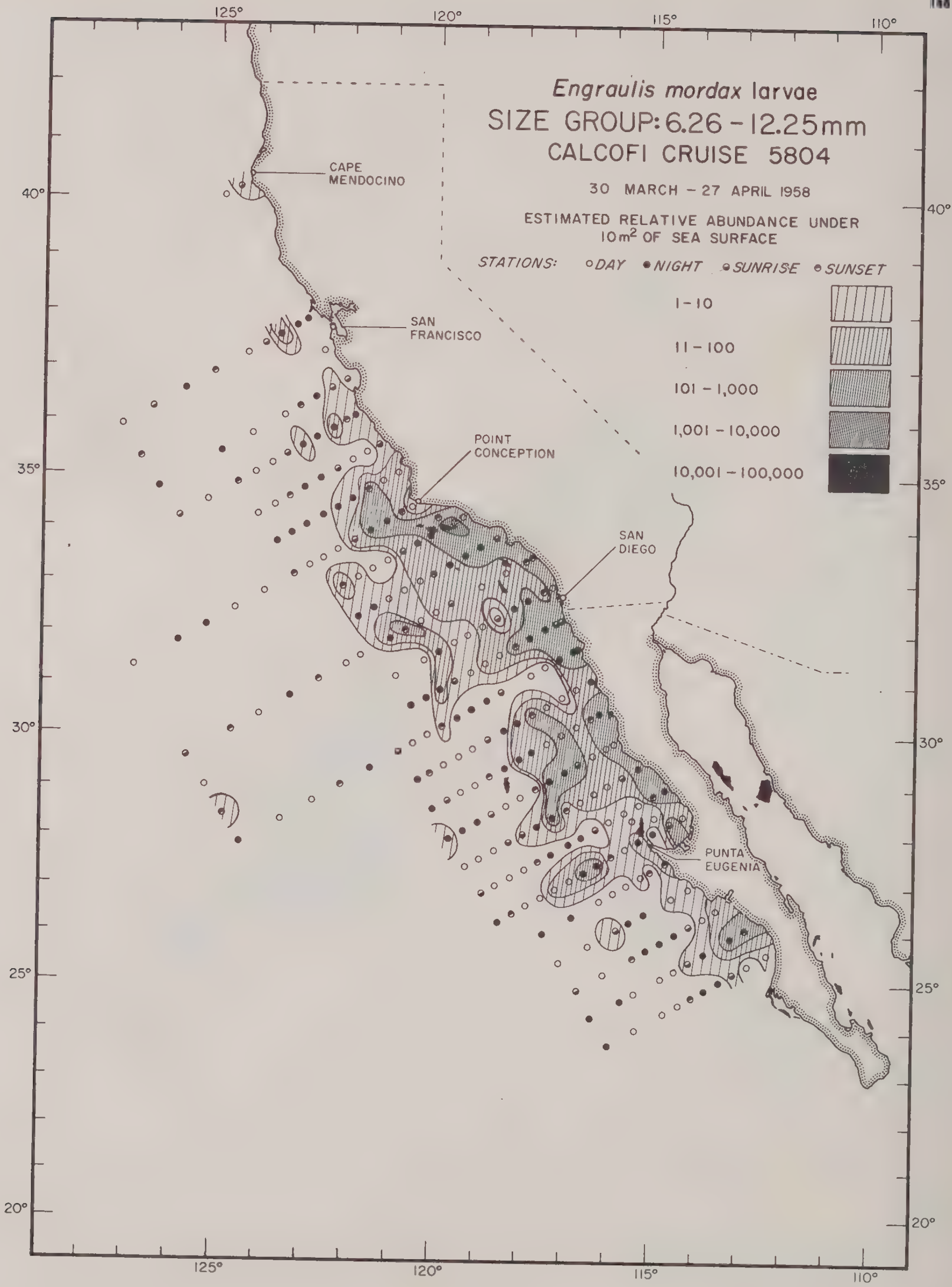


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5803
27 FEBRUARY – 21 MARCH 1958
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◉ SUNRISE ◉ SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

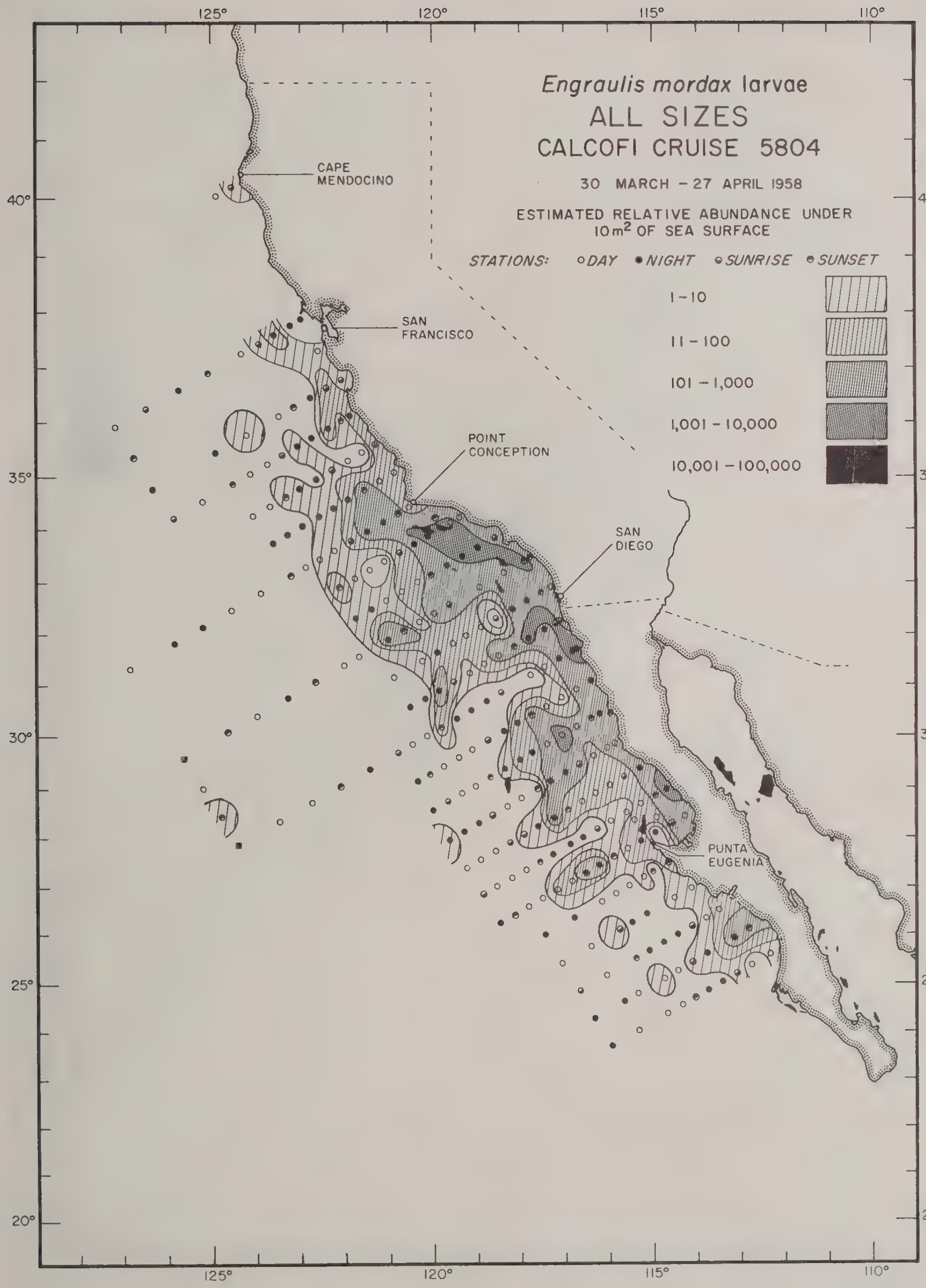
5803


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5804
30 MARCH - 27 APRIL 1958
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◐SUNRISE ◑SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

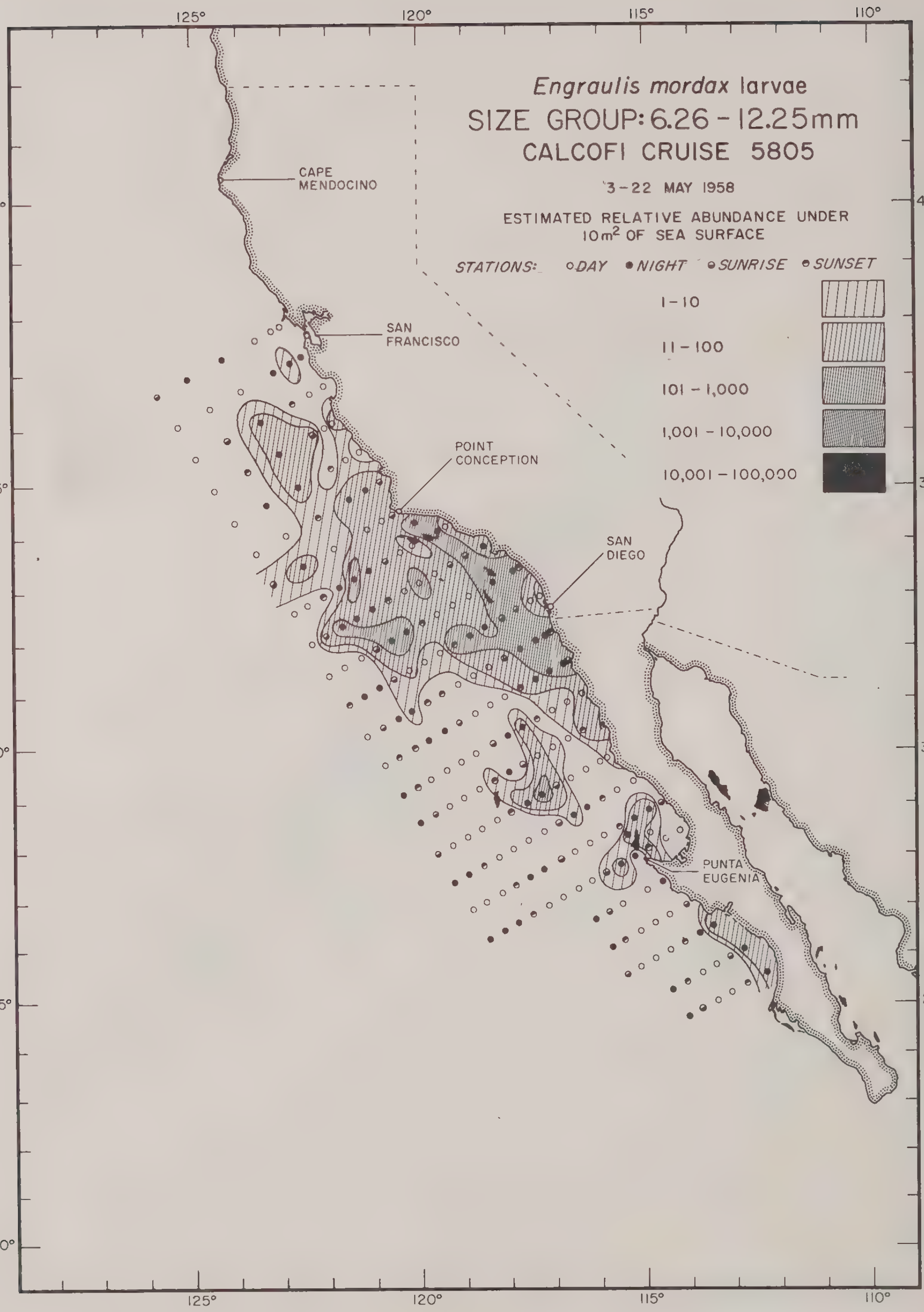
5804


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5804
30 MARCH – 27 APRIL 1958
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

5804

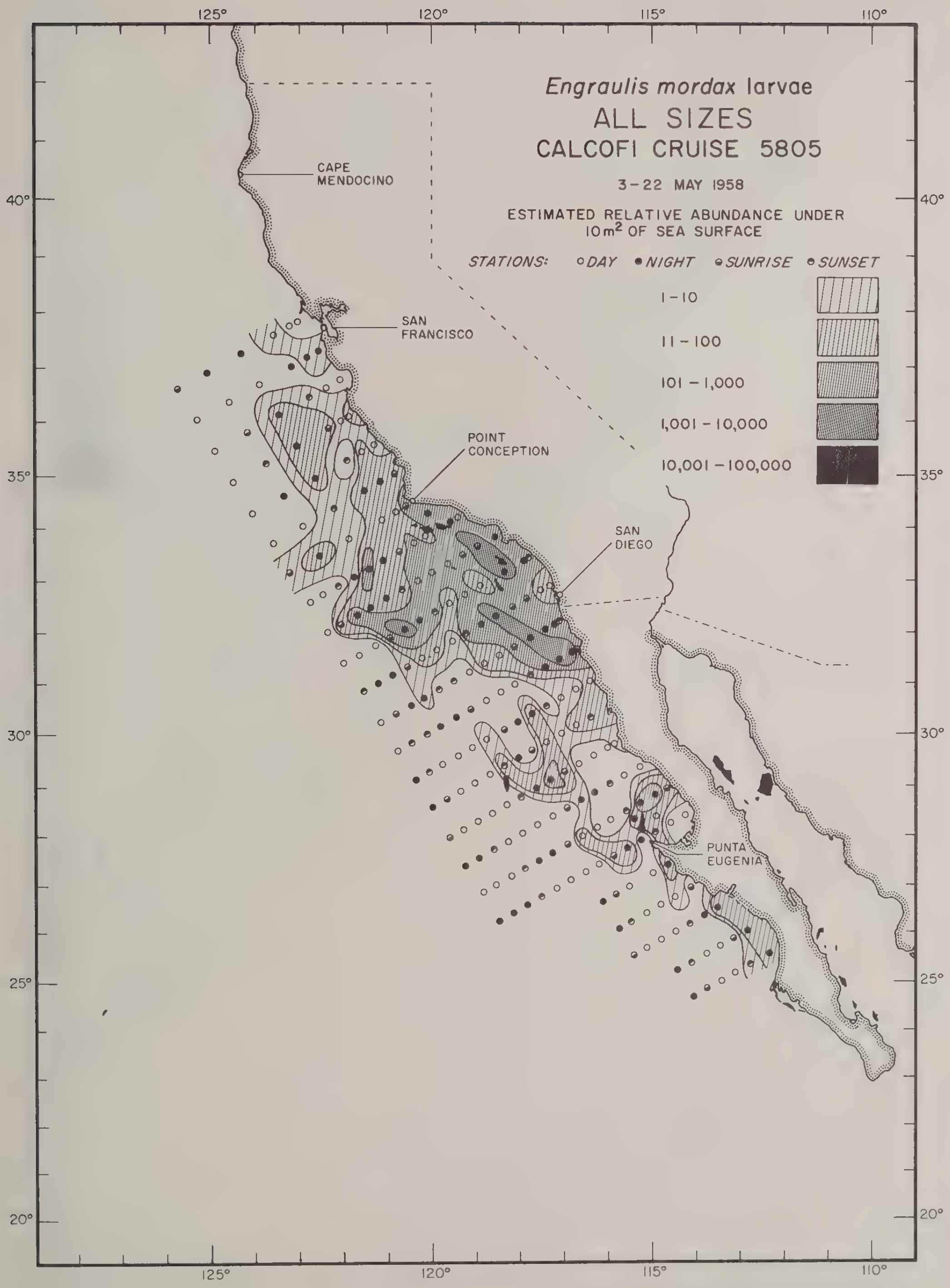


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5805
3-22 MAY 1958
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

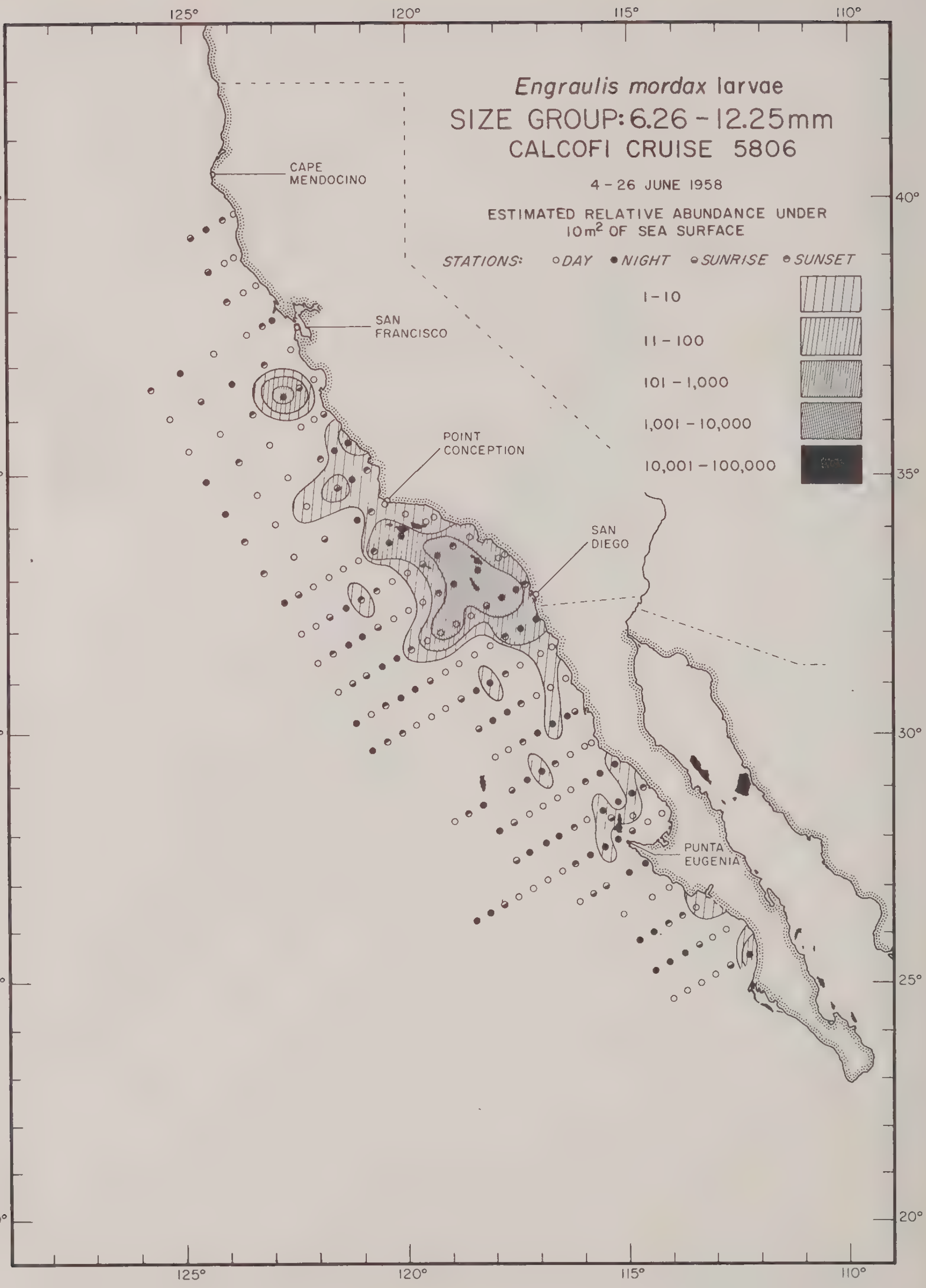
5805


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5805
3–22 MAY 1958
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ *DAY* ● *NIGHT* ◐ *SUNRISE* ◑ *SUNSET*
1–10
11–100
101–1,000
1,001–10,000
10,001–100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

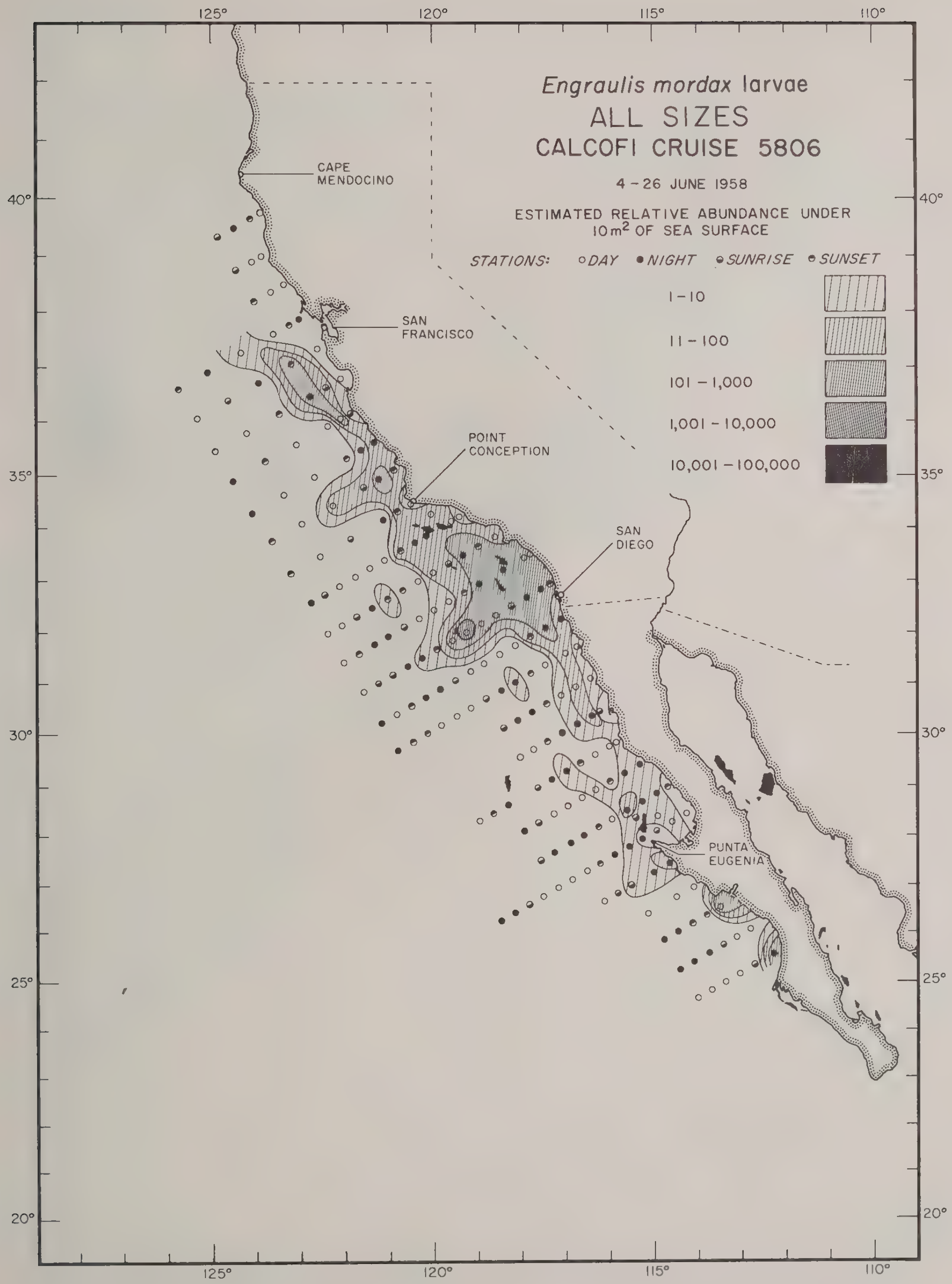
5805


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5806
4 - 26 JUNE 1958
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

Size Group: 6.26-12.25mm

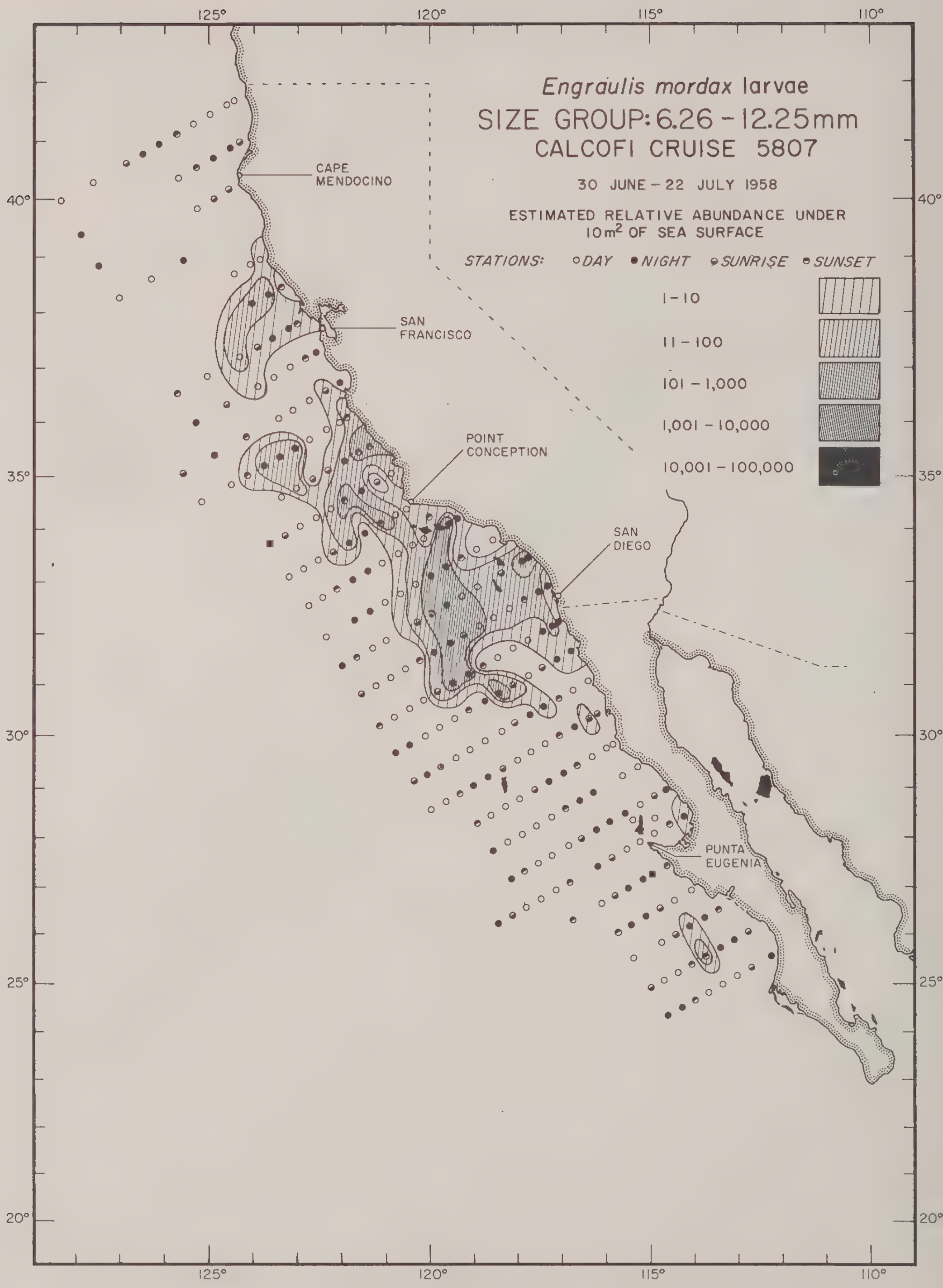
5806


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5806
4 - 26 JUNE 1958
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m^2 OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

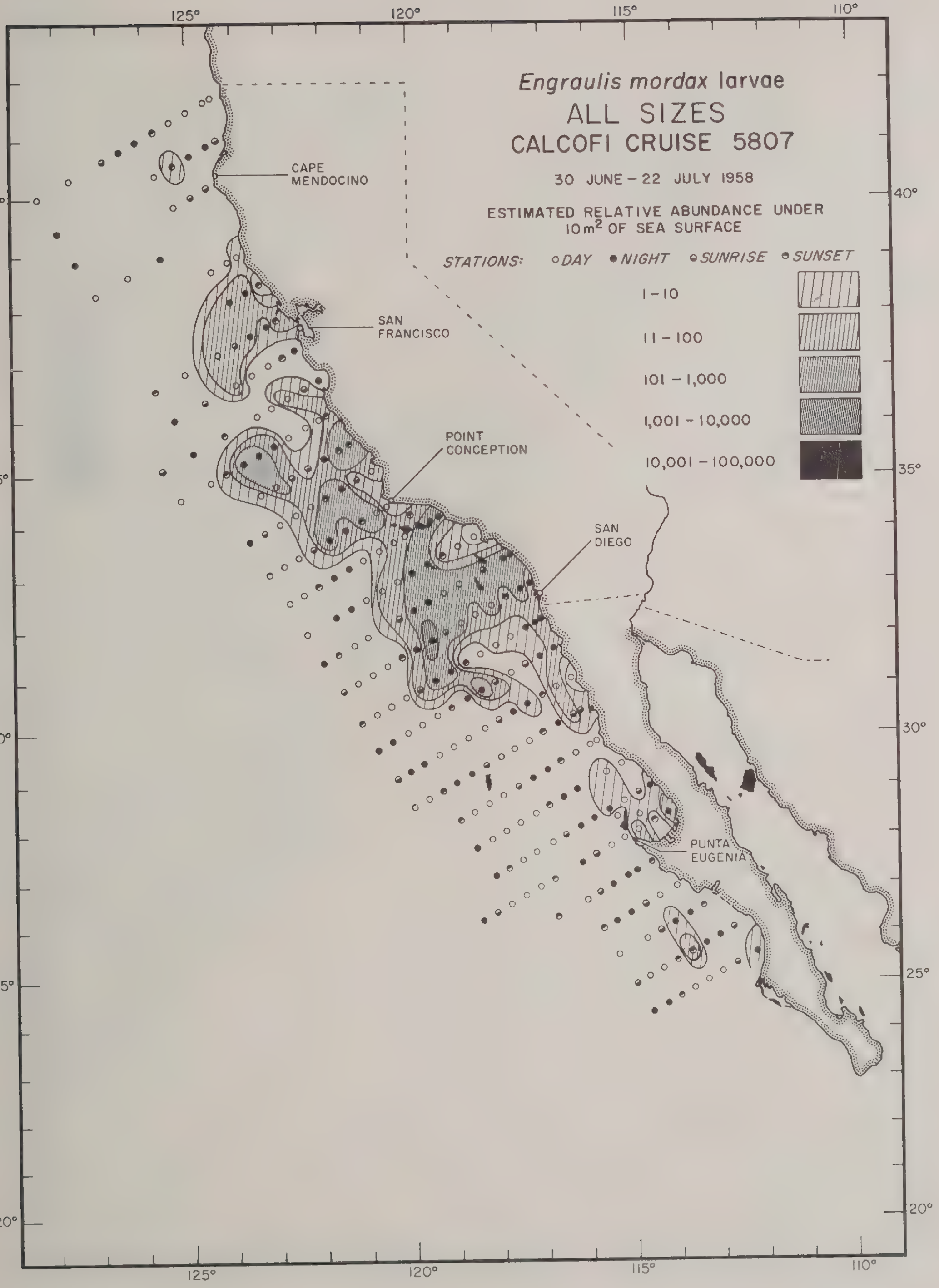
5806


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5807
30 JUNE - 22 JULY 1958
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○*DAY* ●*NIGHT* *SUNRISE* *SUNSET*
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

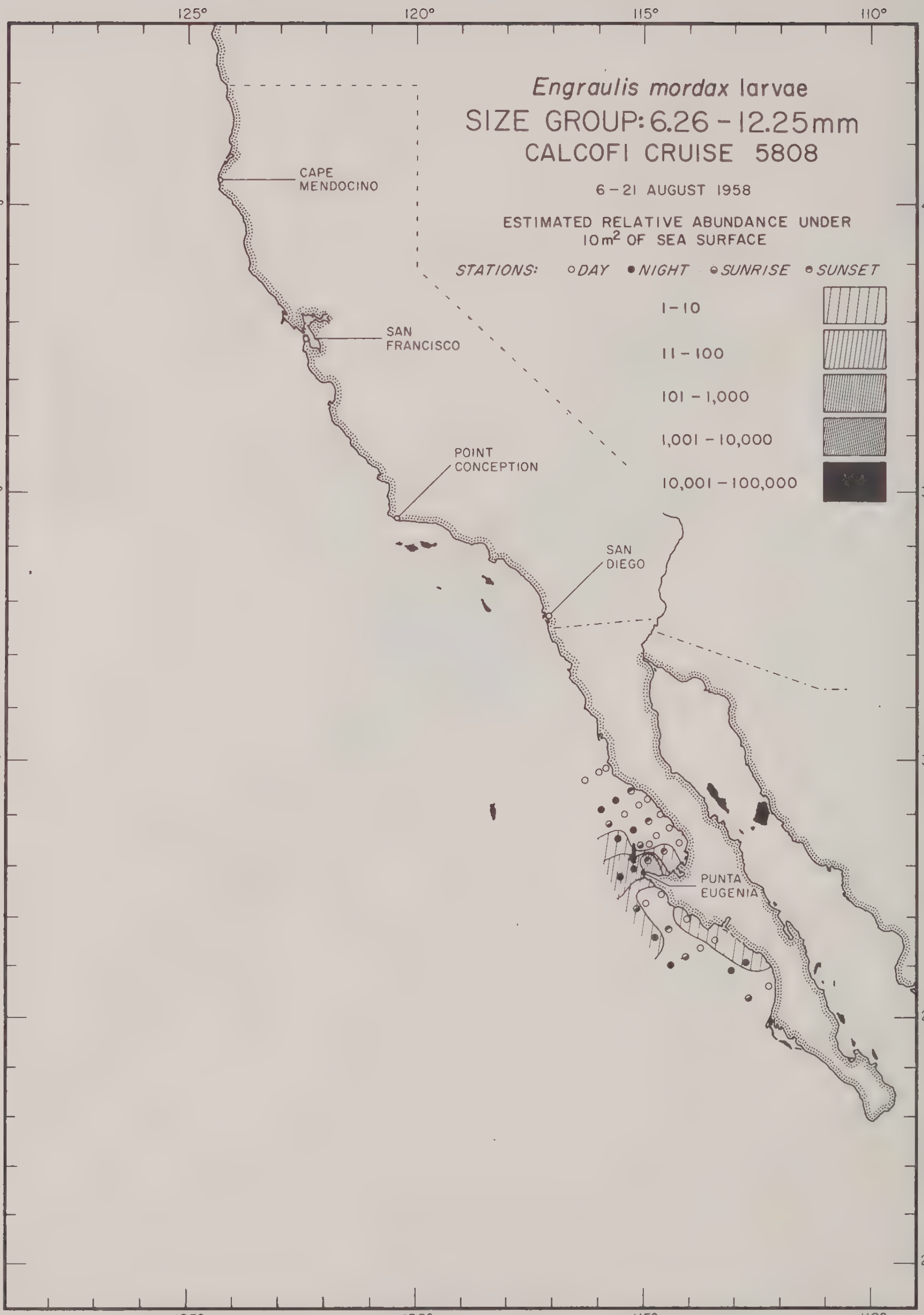
5807


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5807
30 JUNE – 22 JULY 1958
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

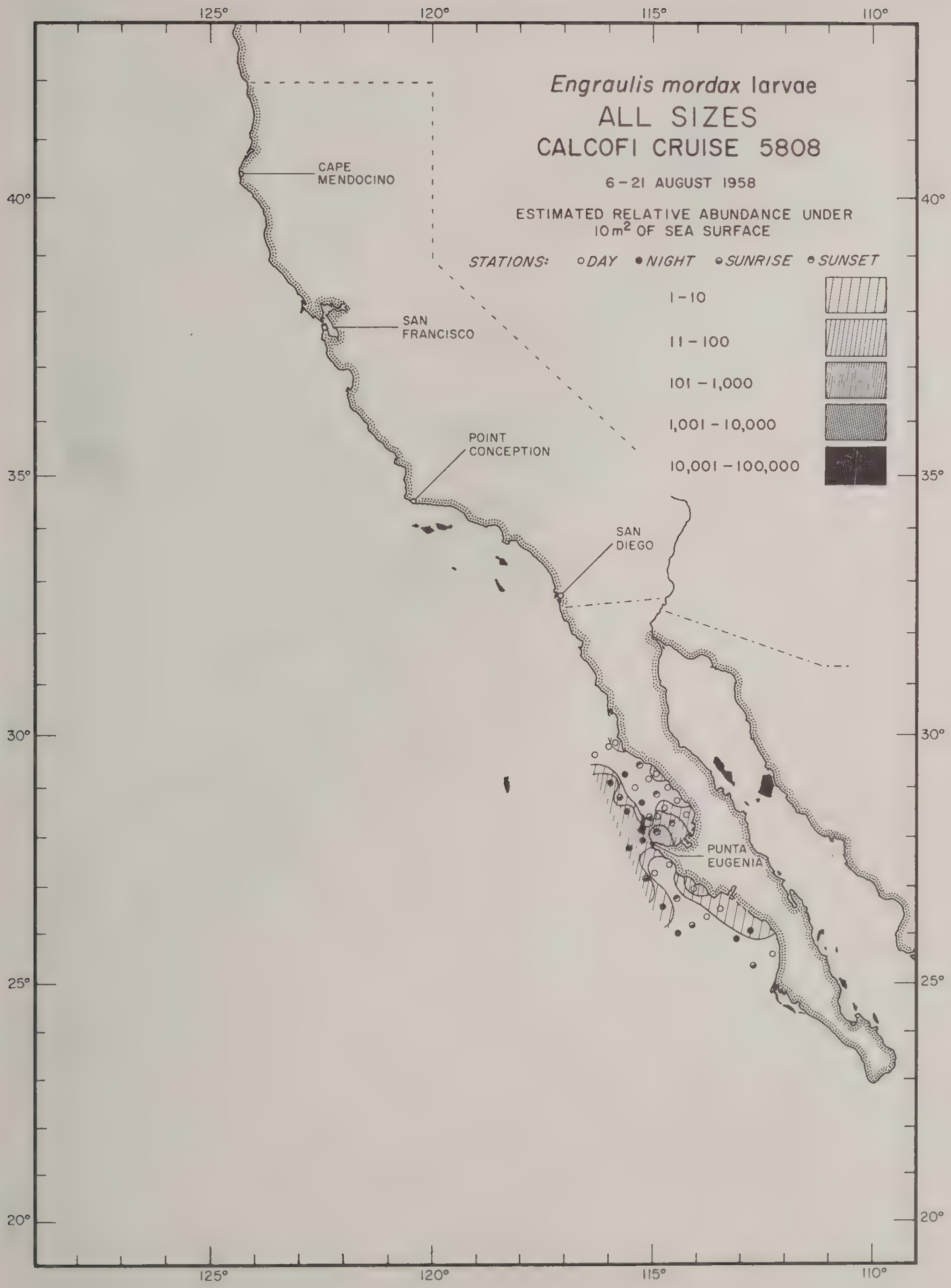
5807


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5808
6 - 21 AUGUST 1958
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ *DAY* ● *NIGHT* *SUNRISE* *SUNSET*
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

Size Group: 6.26-12.25mm

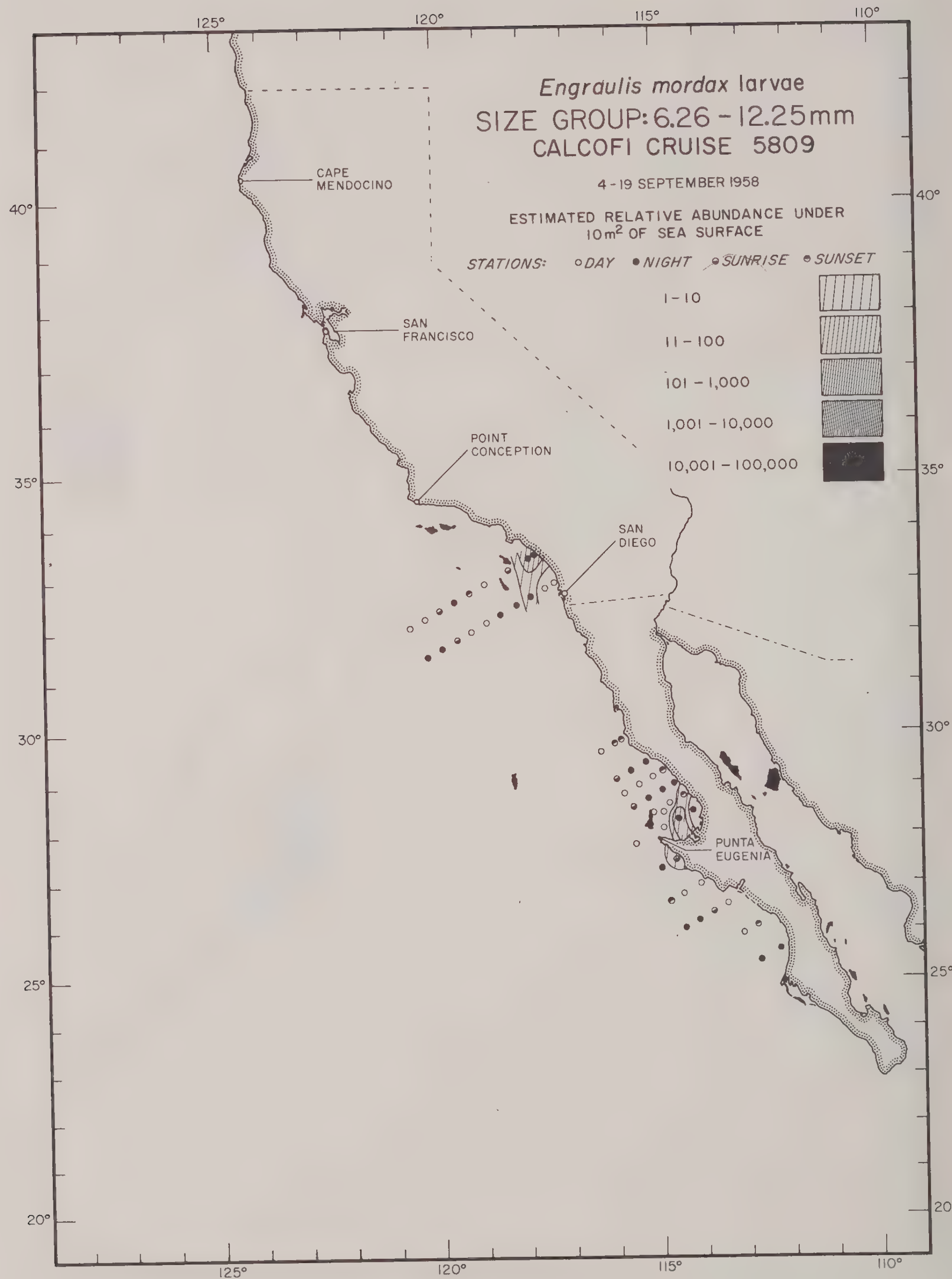
5808


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5808
6-21 AUGUST 1958
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

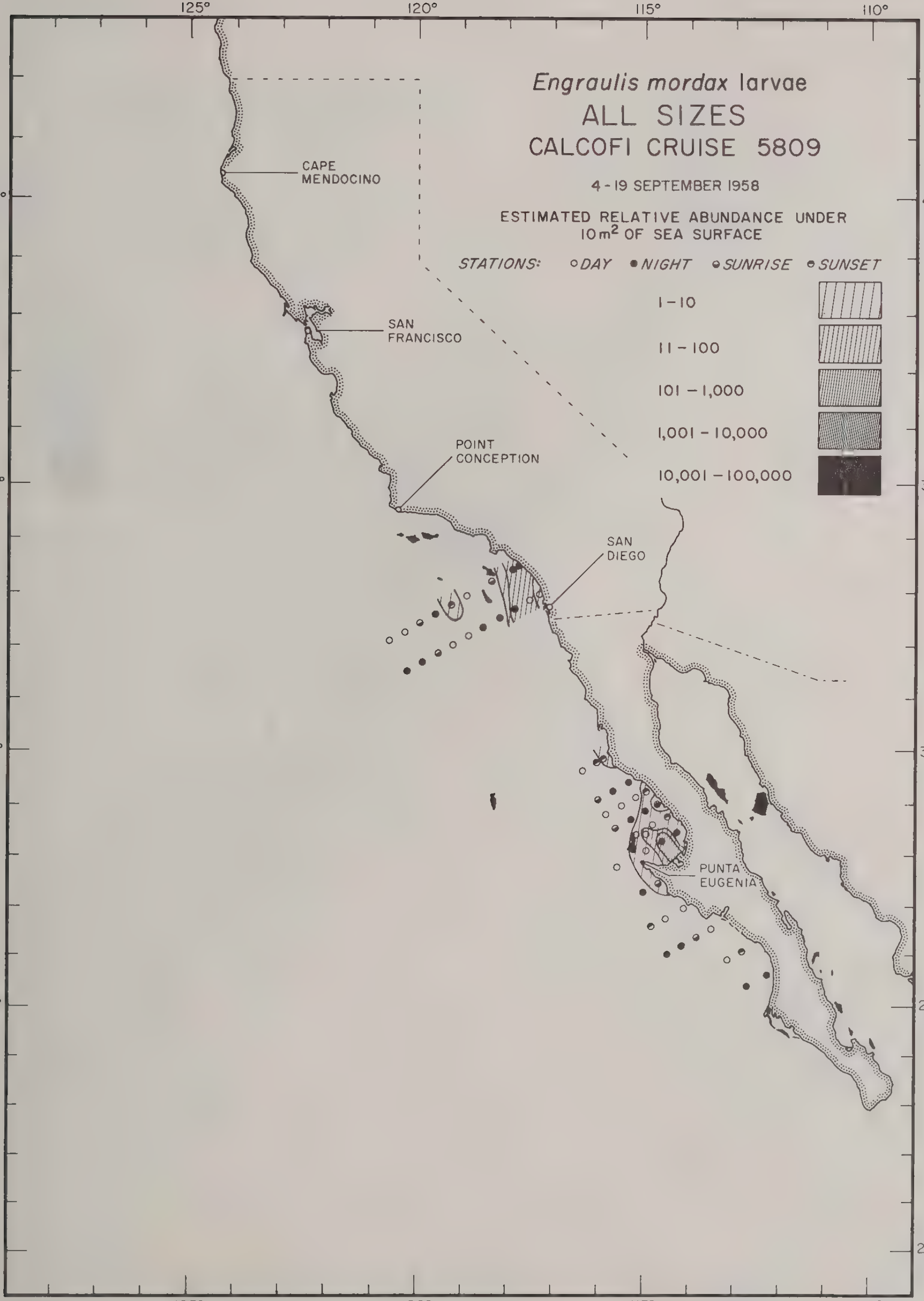
5808


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5809
4 - 19 SEPTEMBER 1958
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

Size Group: 6.26-12.25mm

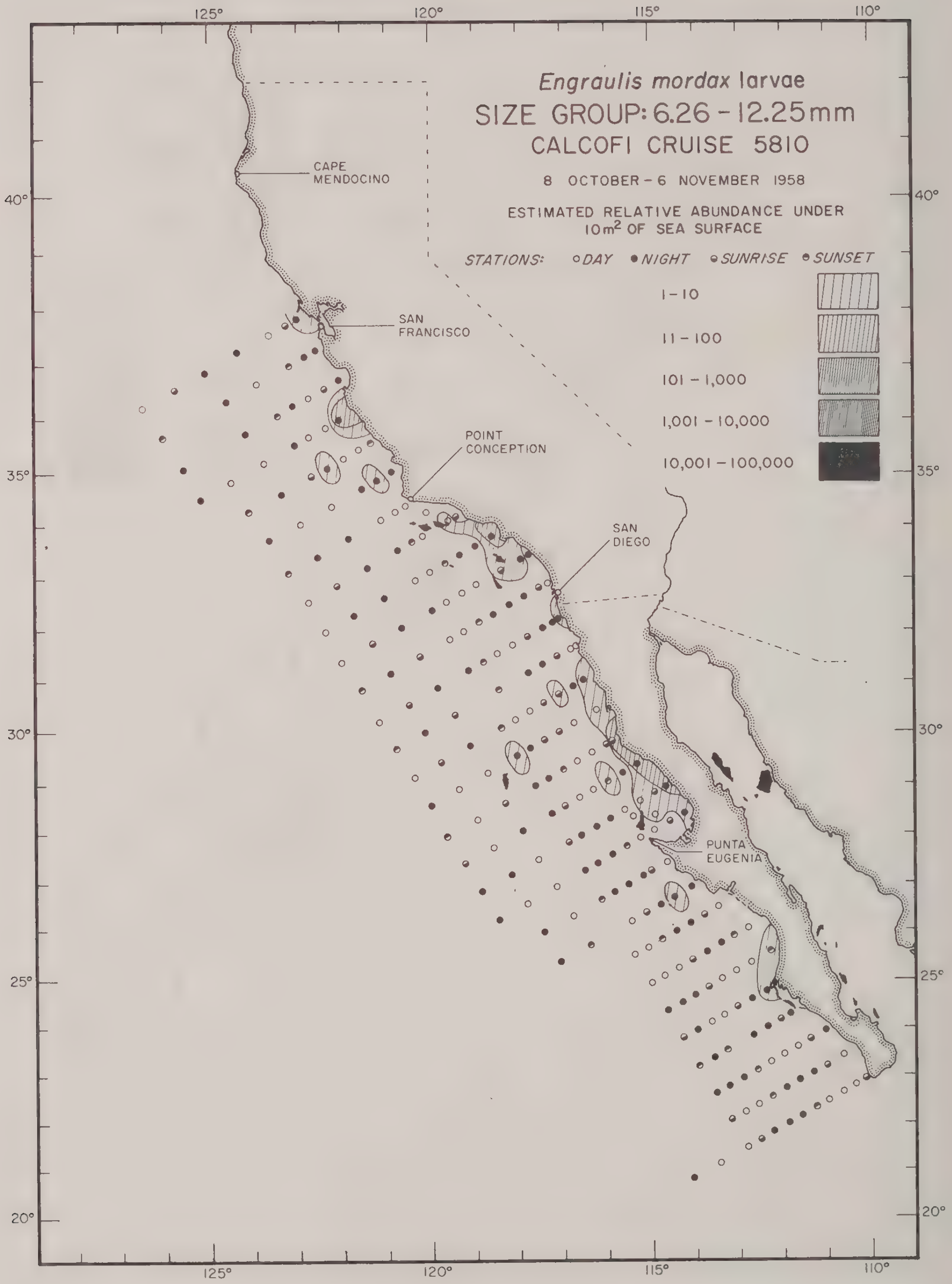
5809


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5809
4 - 19 SEPTEMBER 1958
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ *DAY* ● *NIGHT* *SUNRISE* *SUNSET*
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

All Sizes

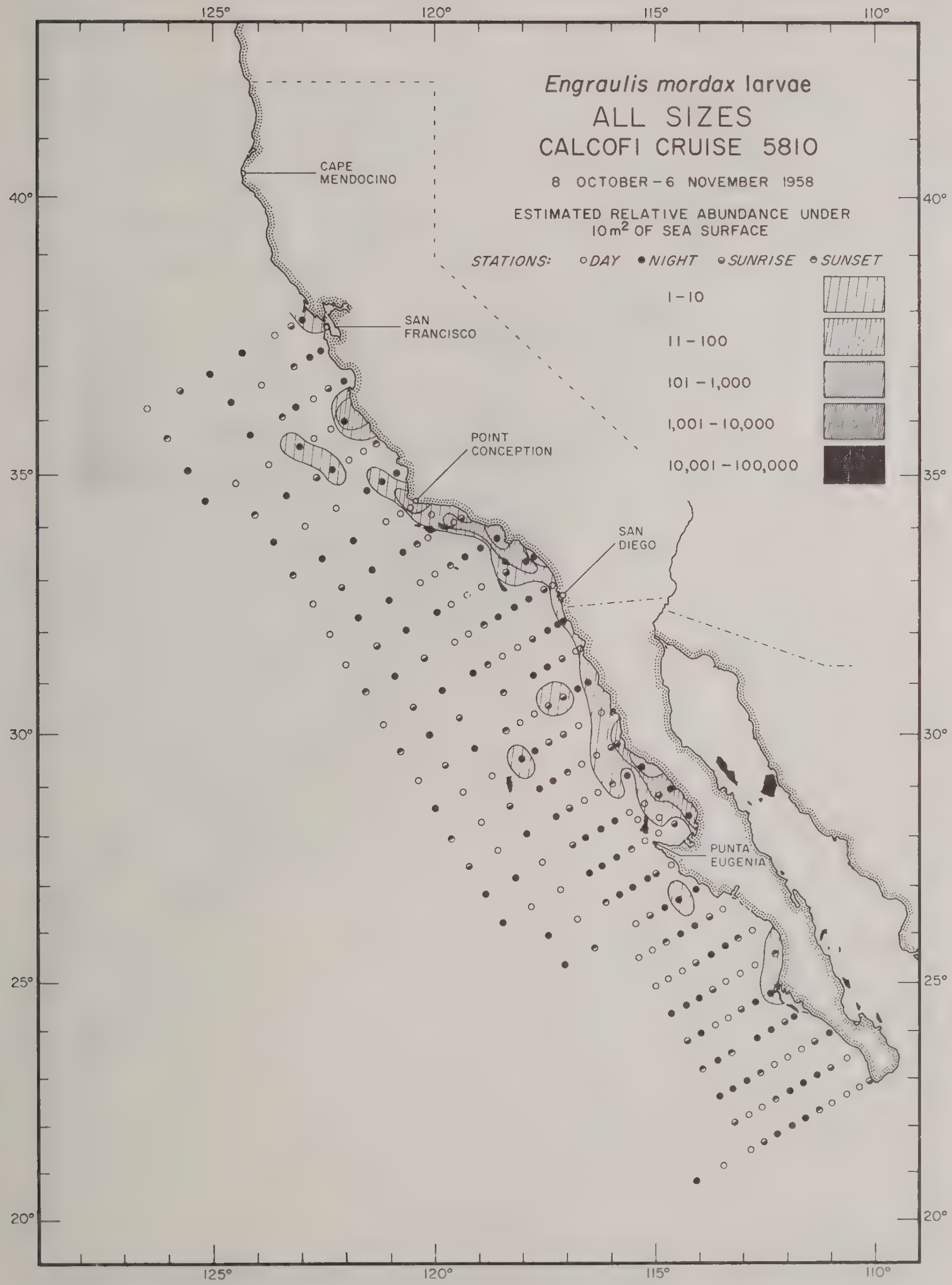
5809


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5810
8 OCTOBER - 6 NOVEMBER 1958
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ *DAY* ● *NIGHT* *SUNRISE* *SUNSET*
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

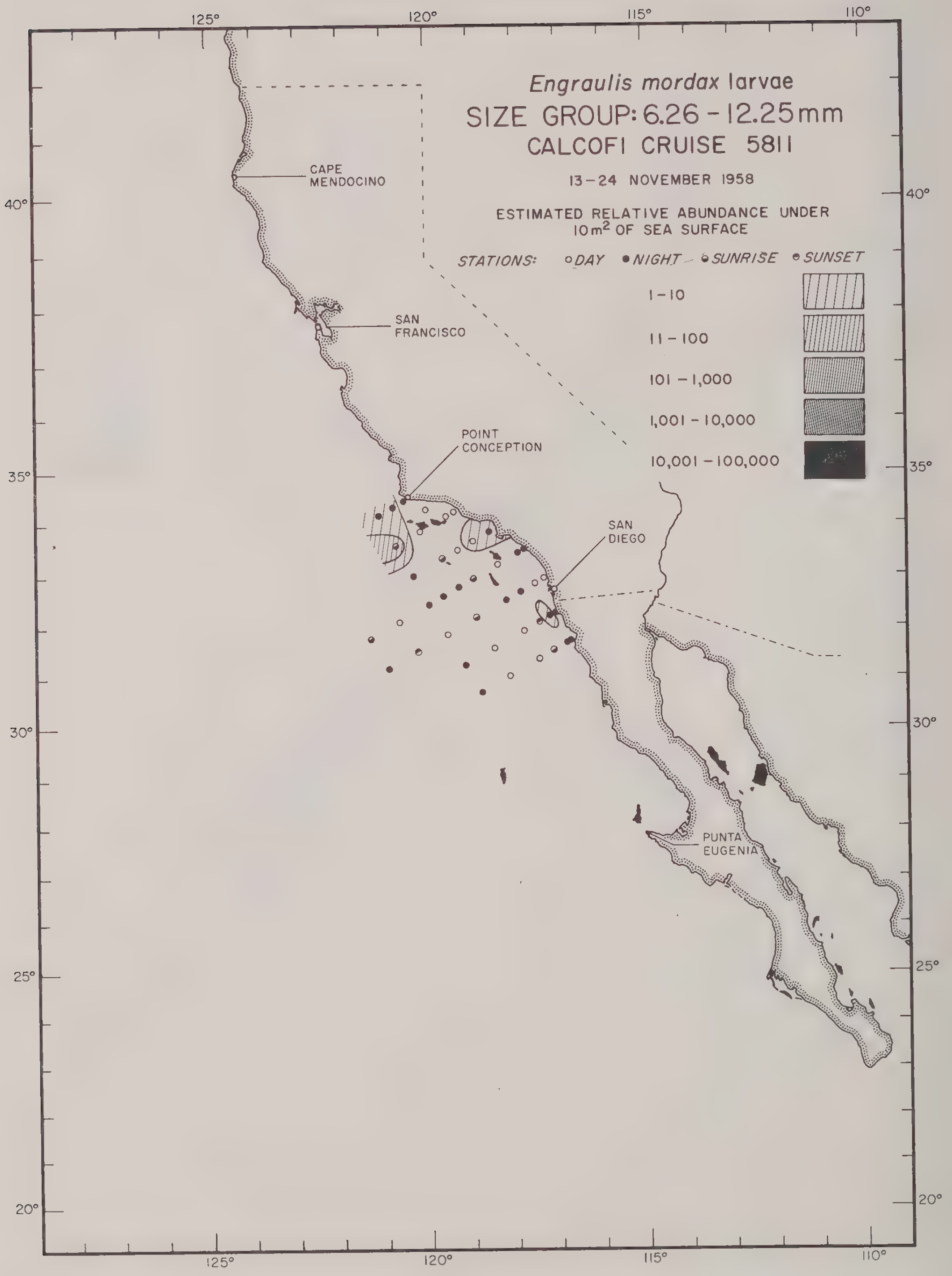
5810


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5810
8 OCTOBER – 6 NOVEMBER 1958
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

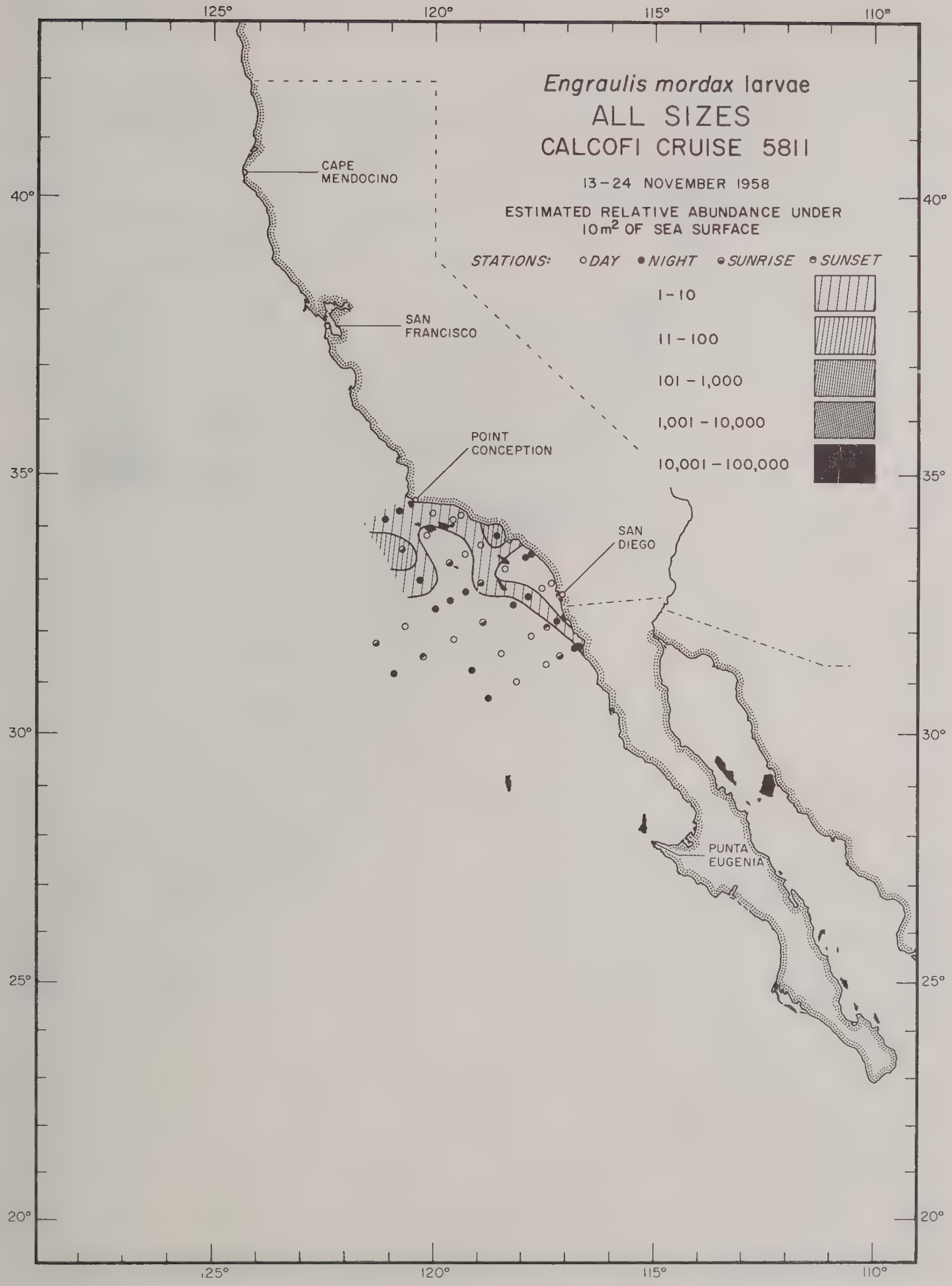
5810


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5811
13-24 NOVEMBER 1958
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25 mm

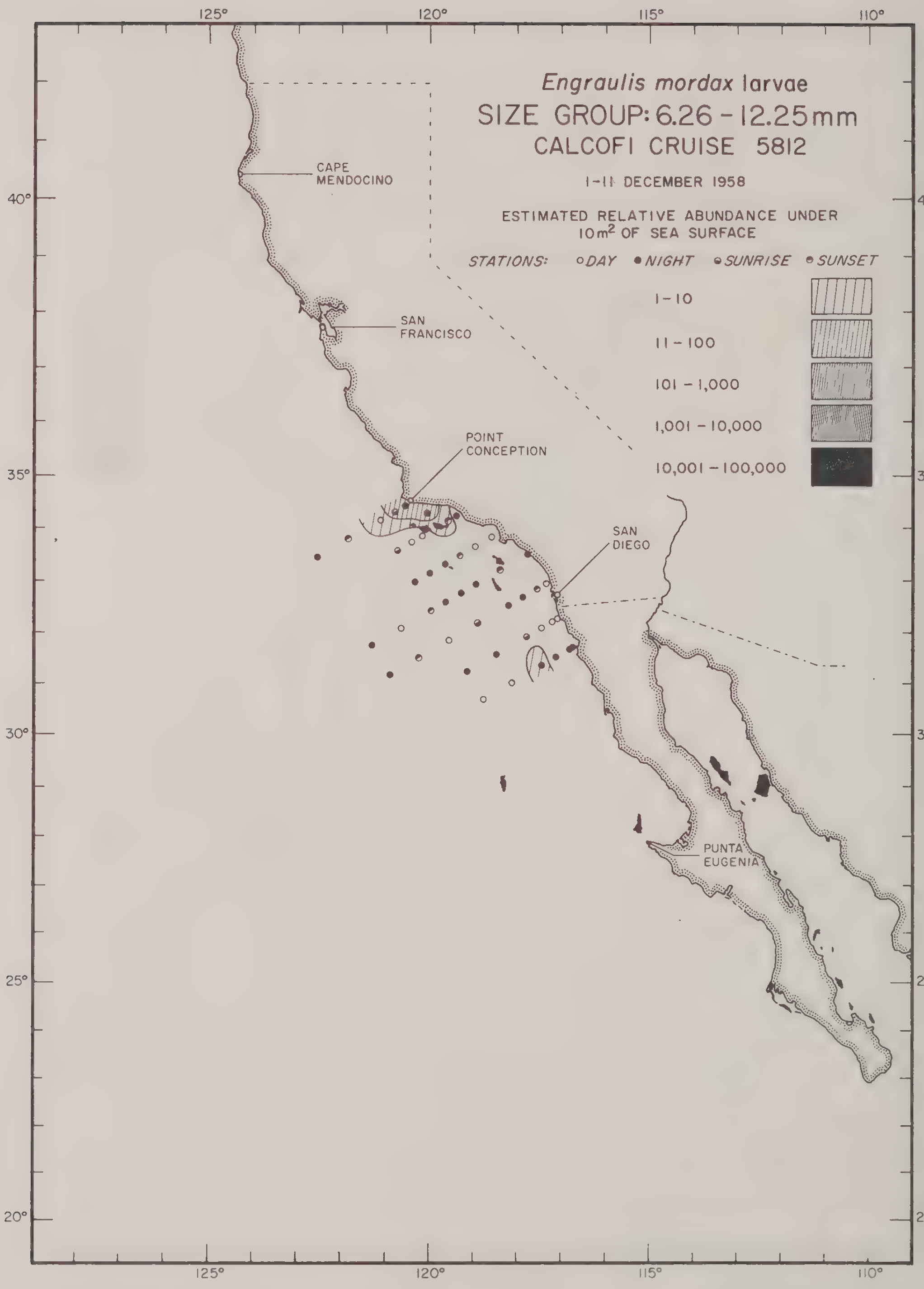
5811


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5811
13–24 NOVEMBER 1958
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

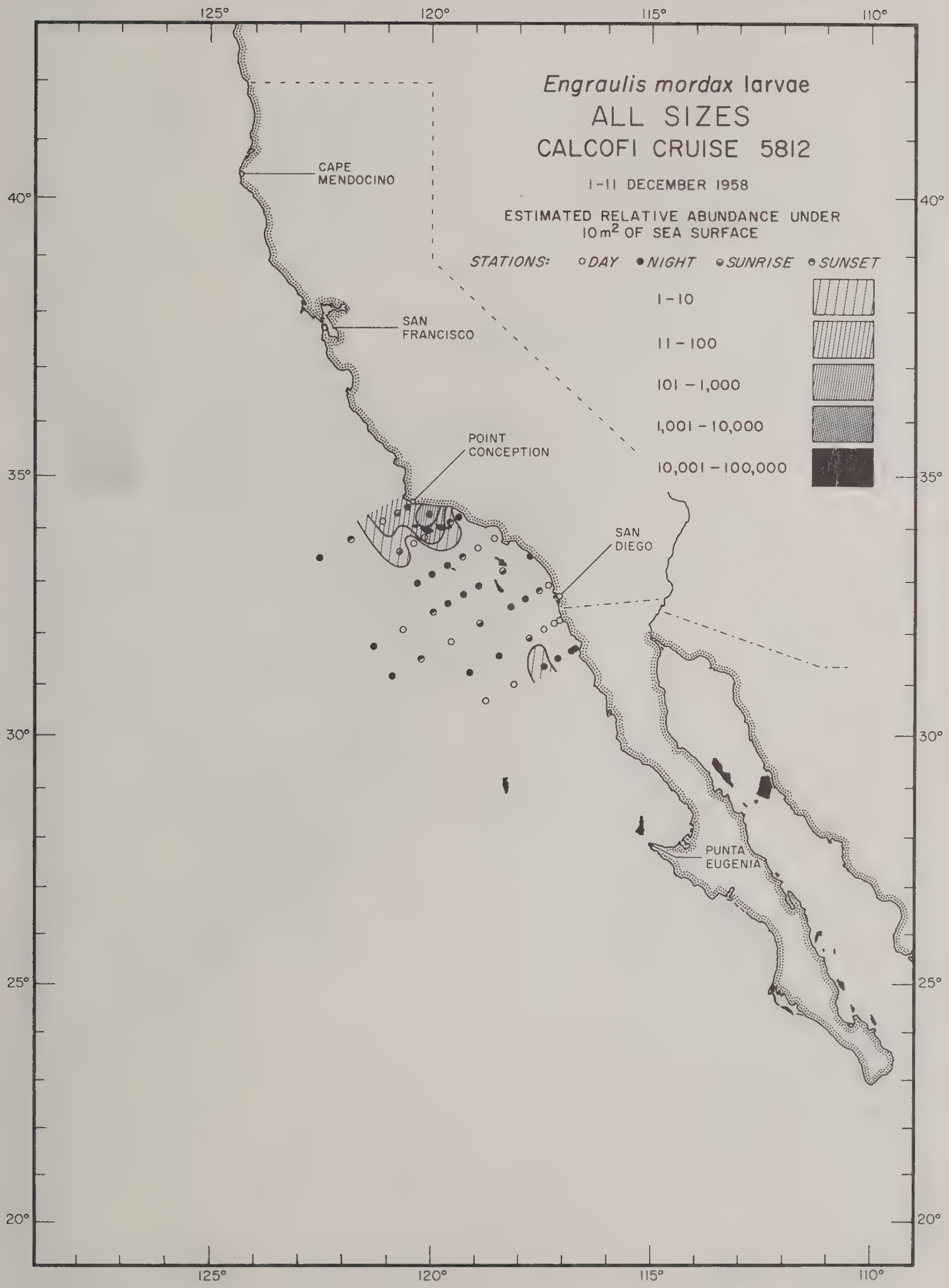
5811


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5812
1-11 DECEMBER 1958
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ *DAY* ● *NIGHT* *SUNRISE* *SUNSET*
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

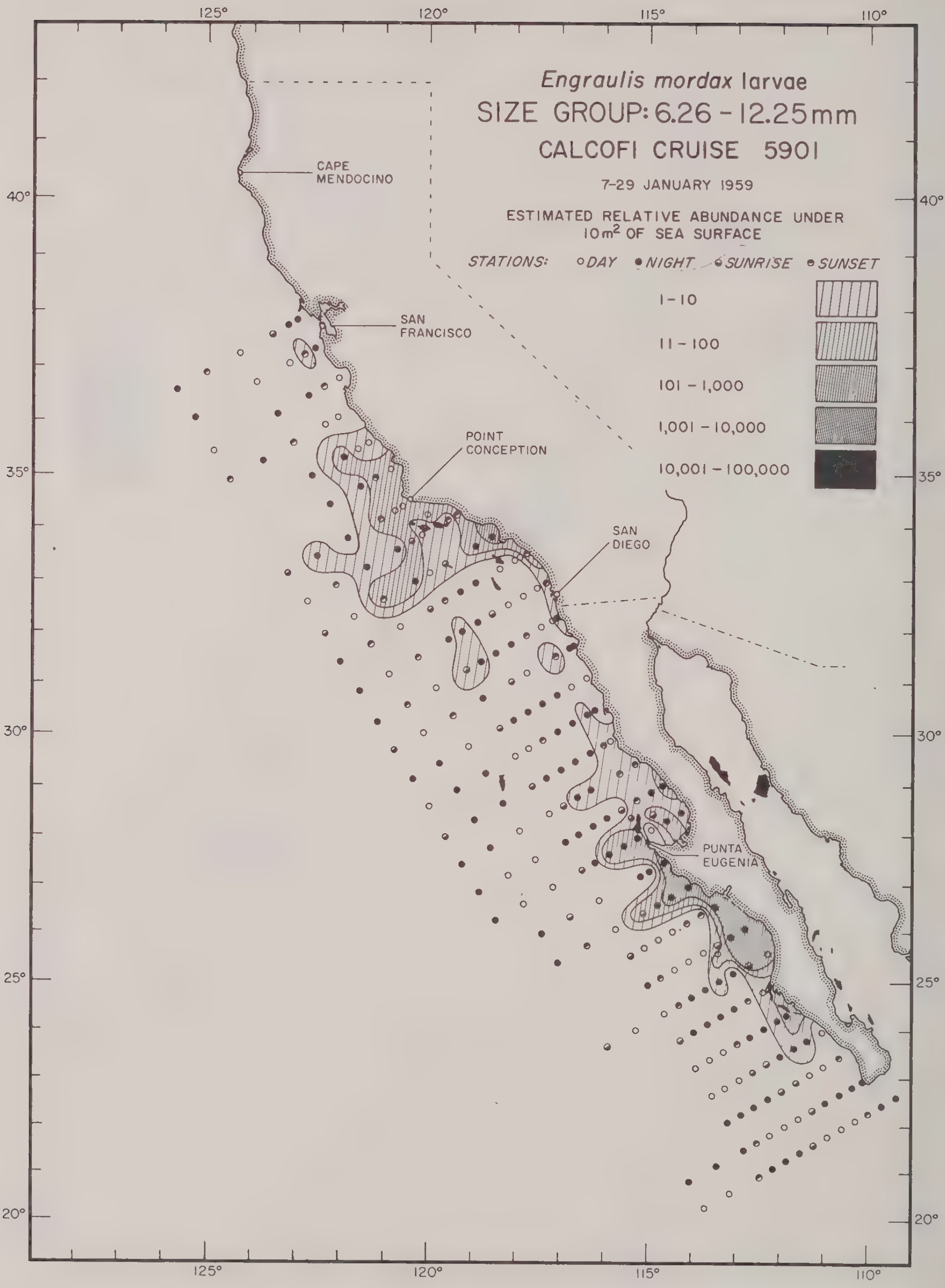
5812


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5812
1-11 DECEMBER 1958
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

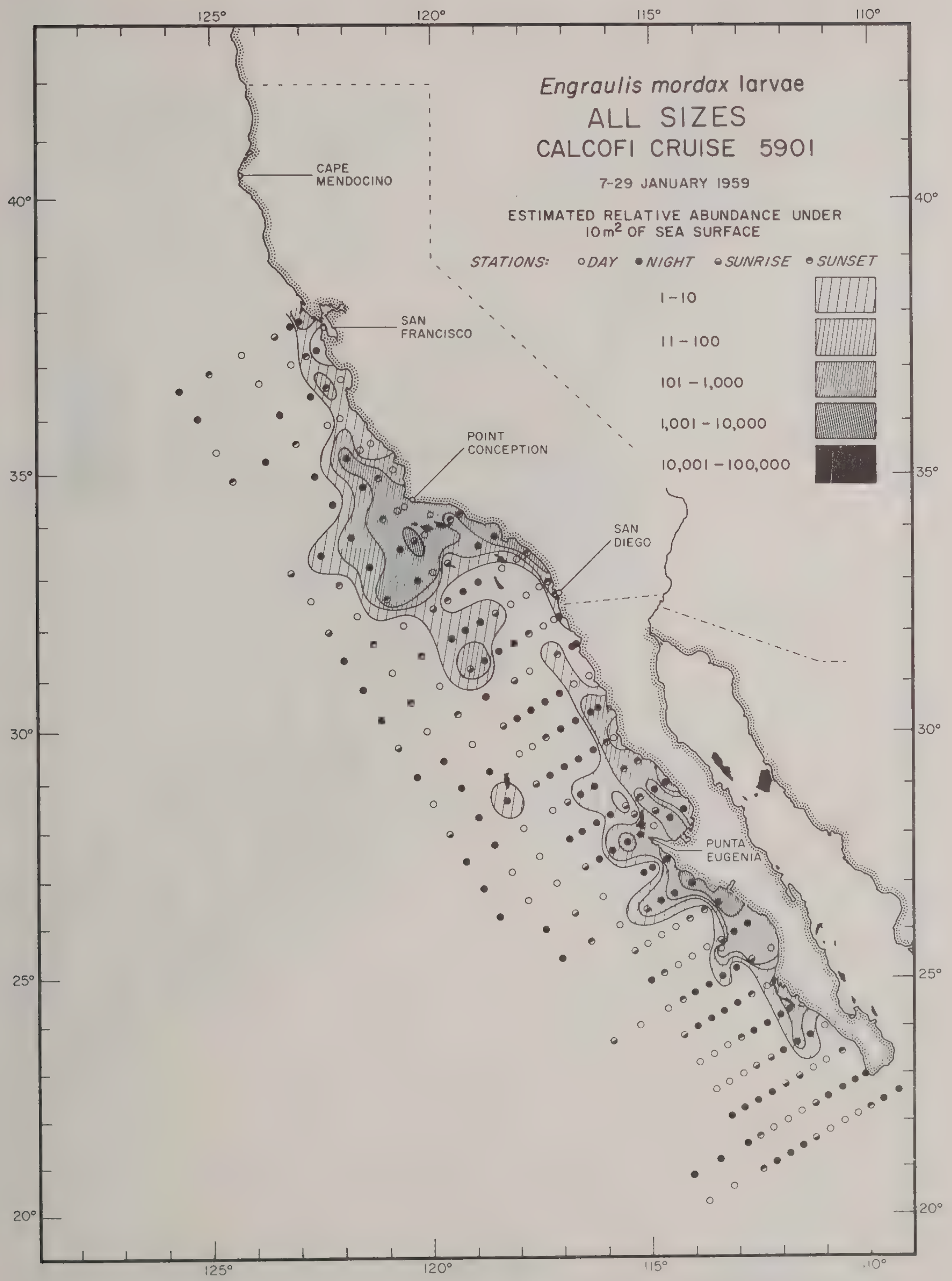
5812


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5901
7-29 JANUARY 1959
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◐SUNRISE ◒SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

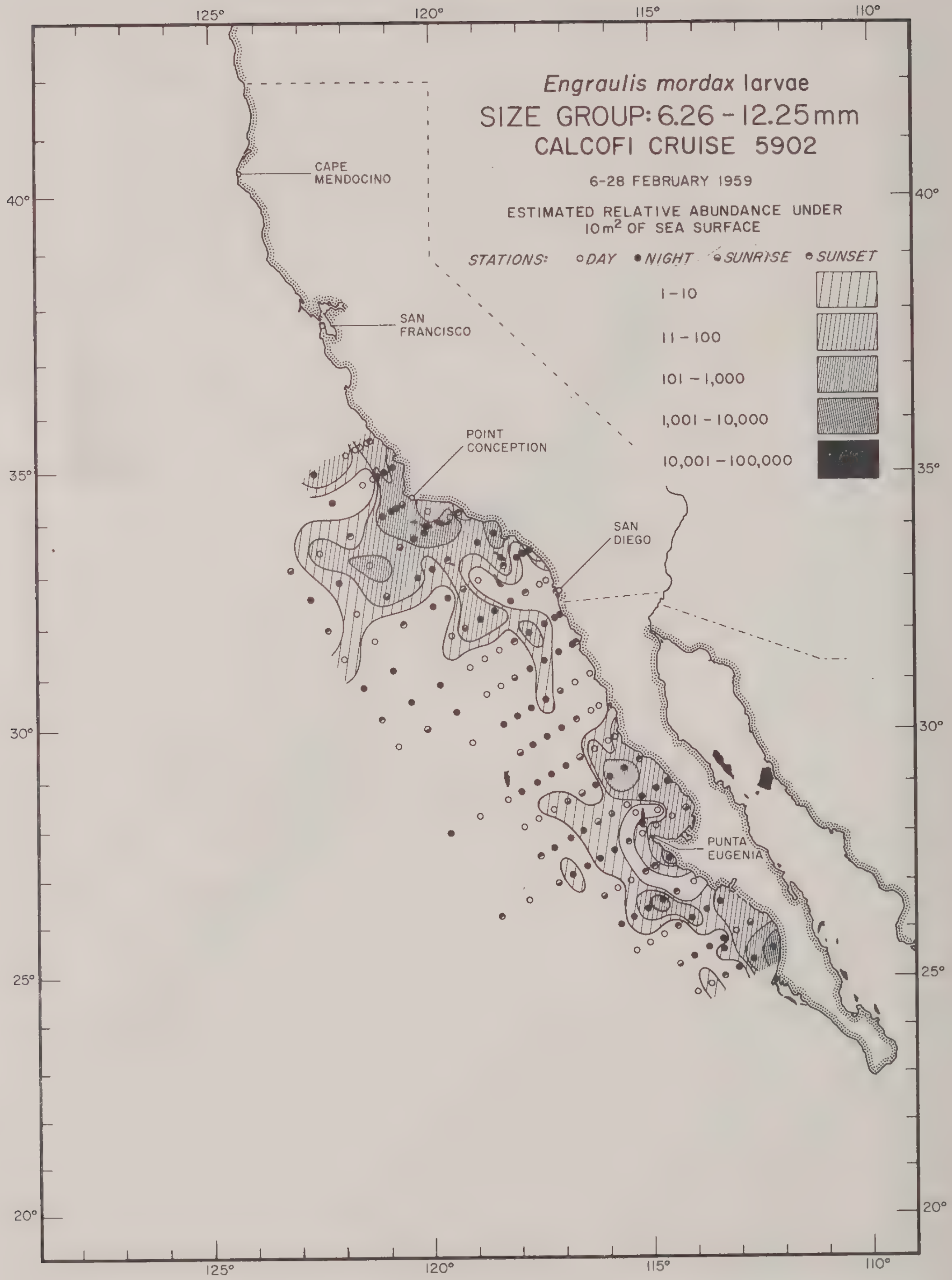
5901


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5901
7-29 JANUARY 1959
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

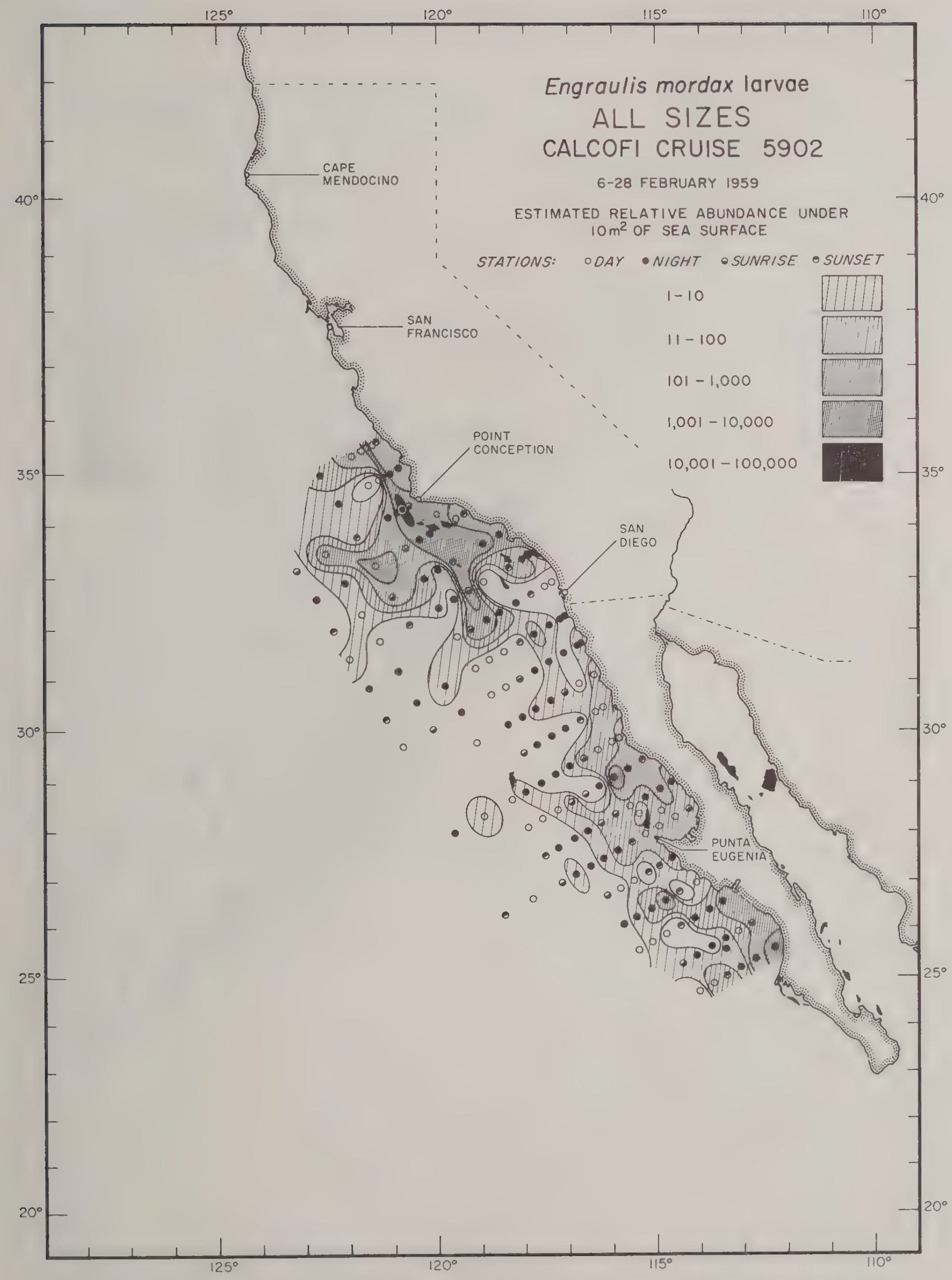
5901


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5902
6-28 FEBRUARY 1959
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

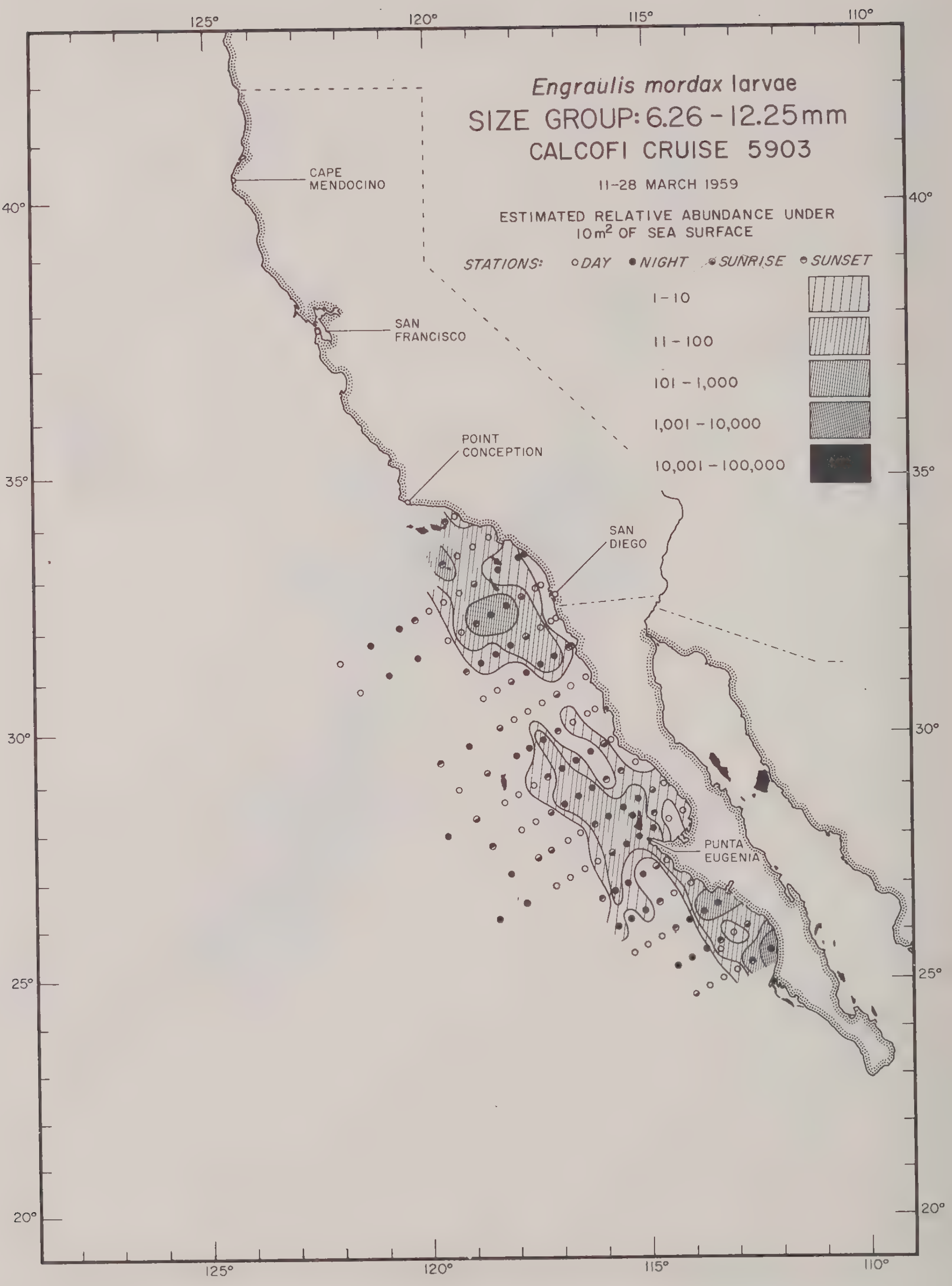
5902


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5902
6-28 FEBRUARY 1959
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

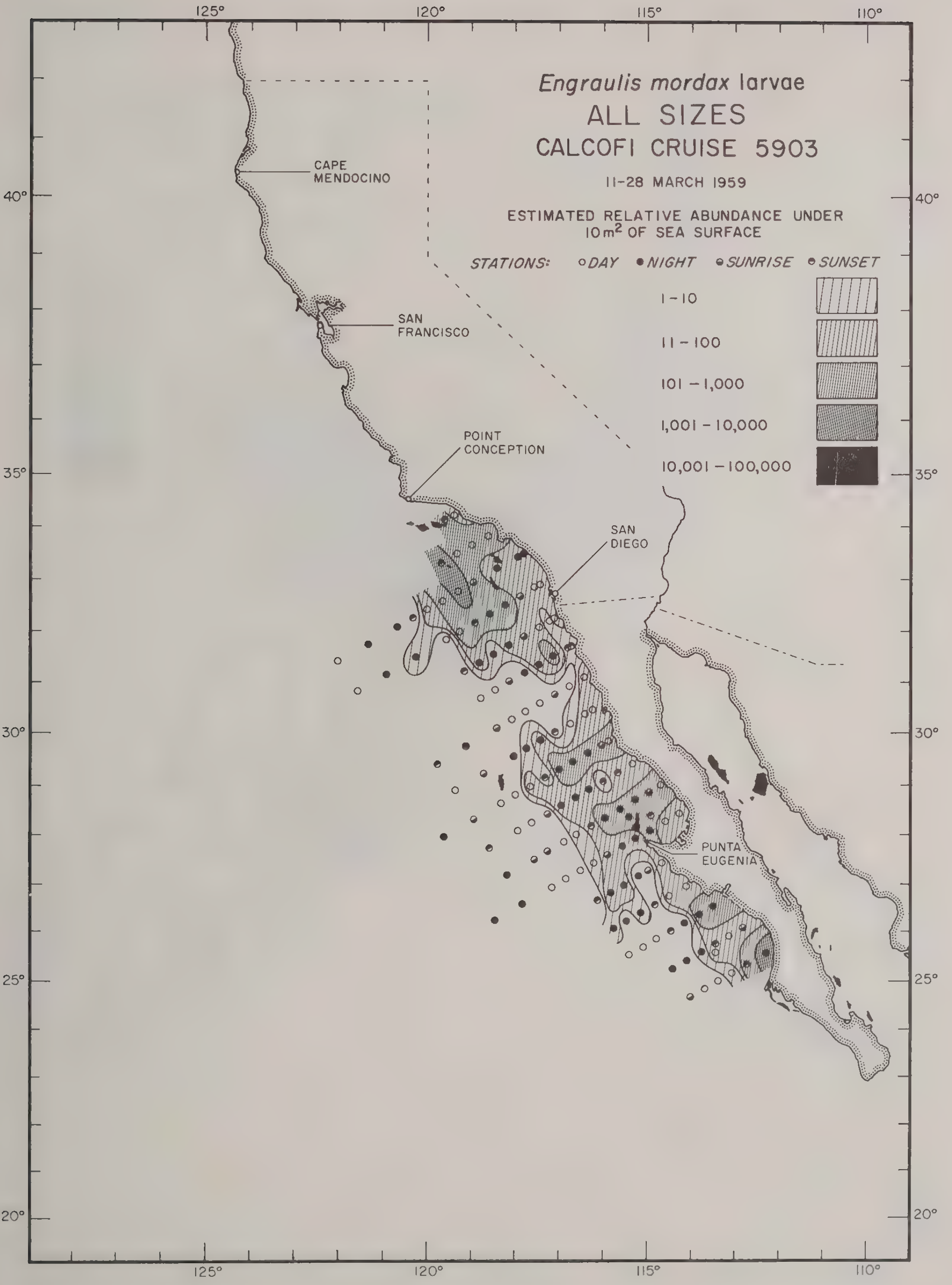
5902


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5903
11-28 MARCH 1959
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

5903

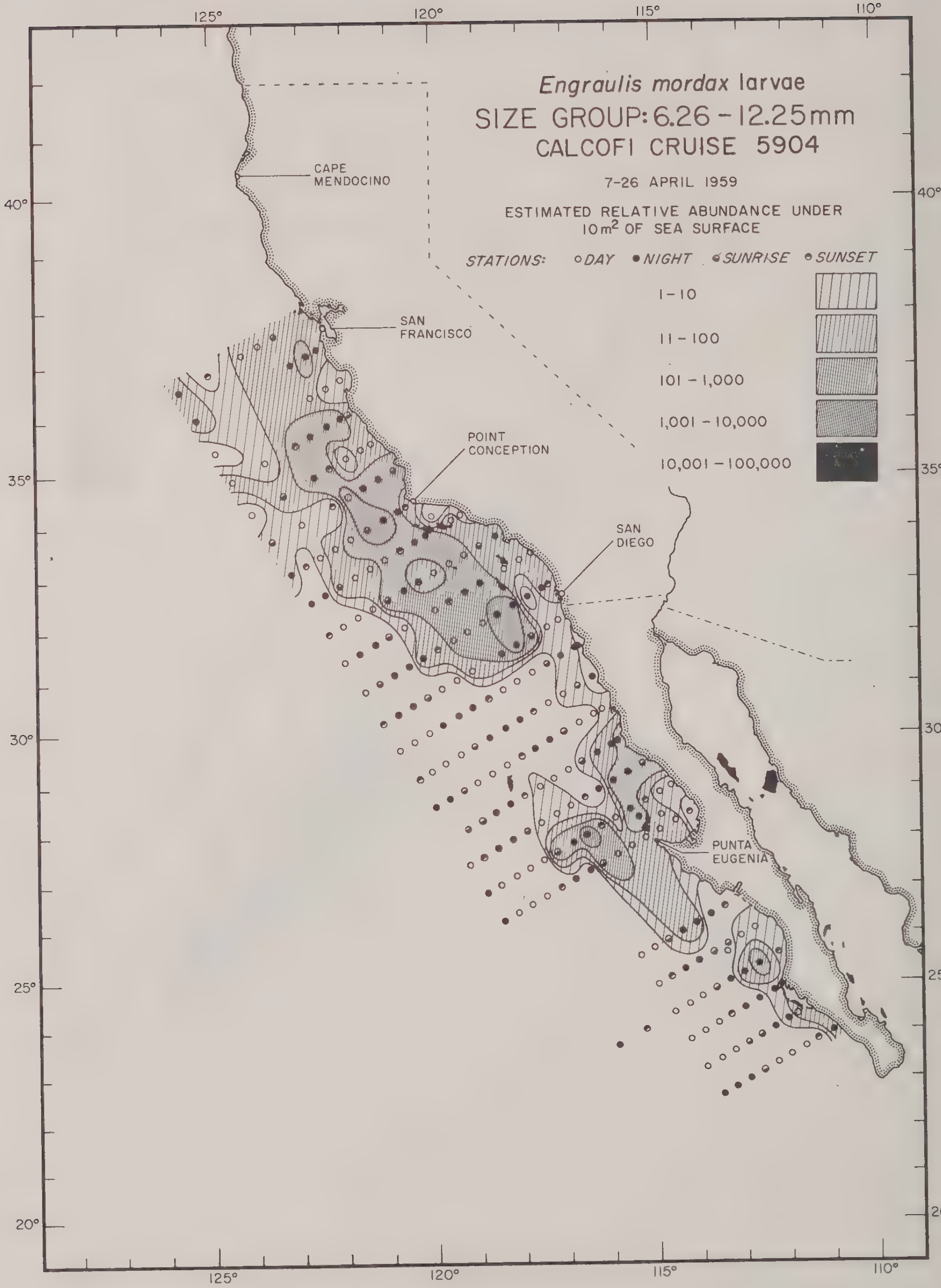


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5903
11-28 MARCH 1959
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT SUNRISE SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

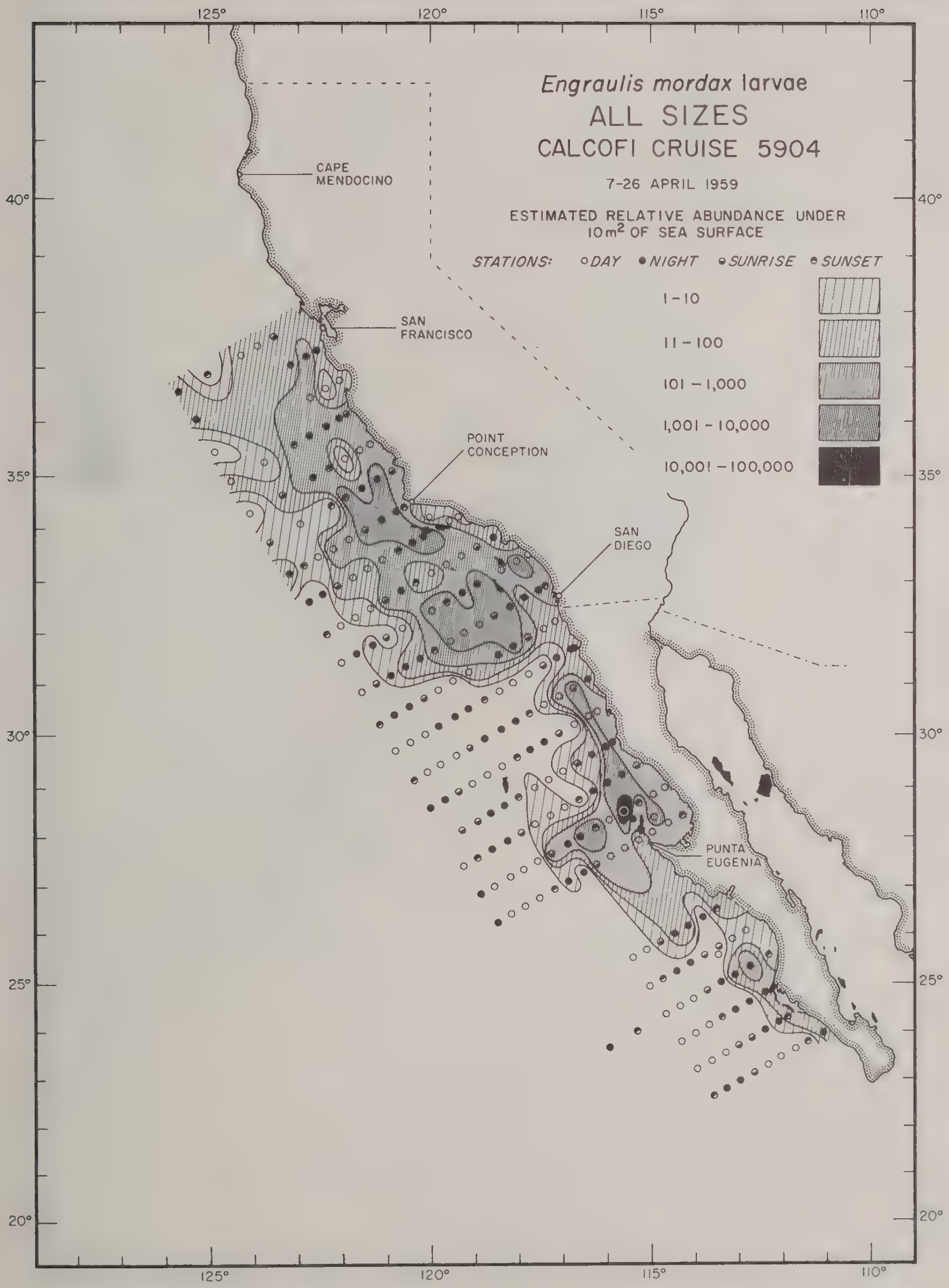
5903


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5904
7-26 APRIL 1959
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◐SUNRISE ◑SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

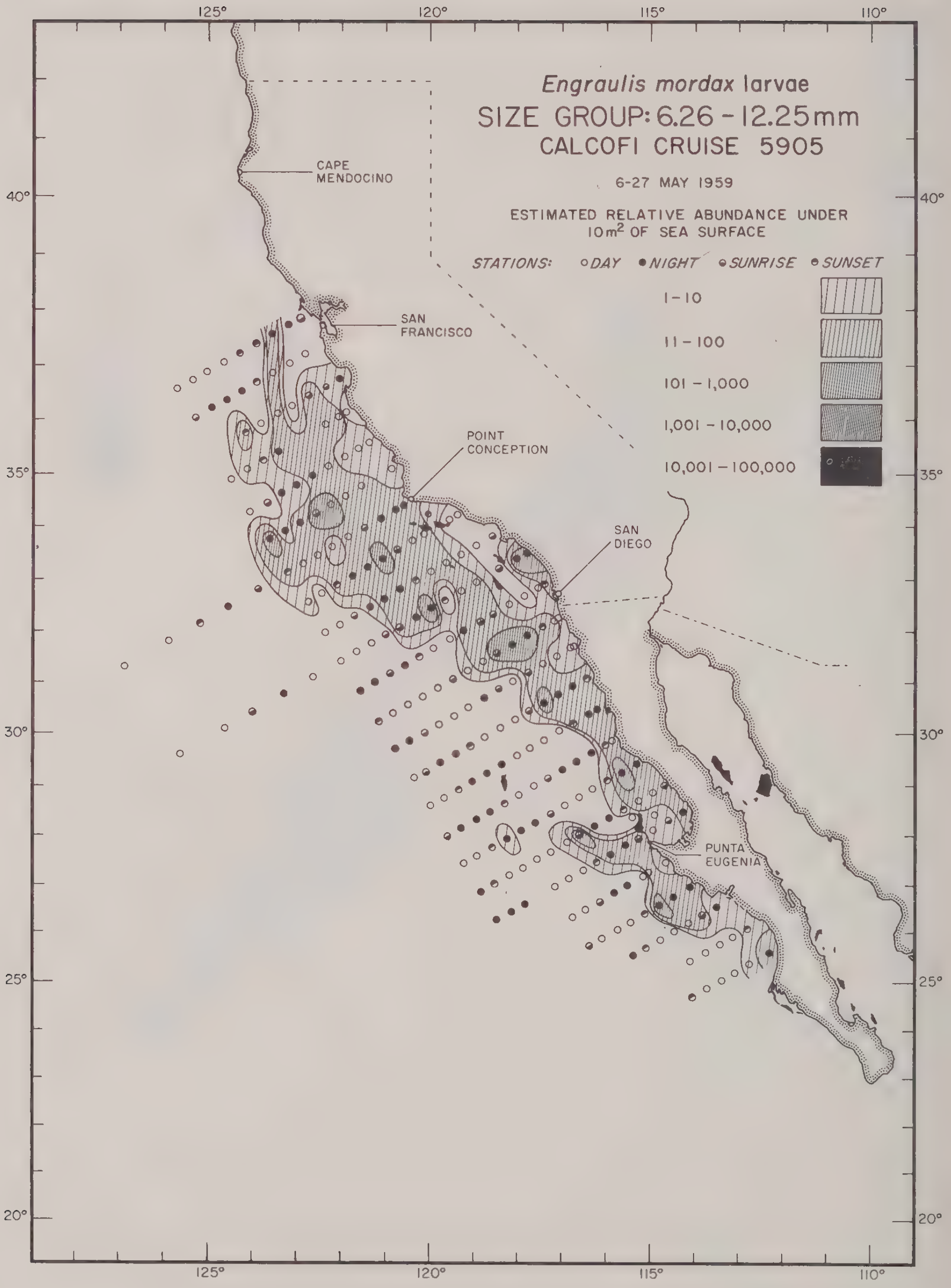
5904


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5904
7-26 APRIL 1959
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◐SUNRISE ◑SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

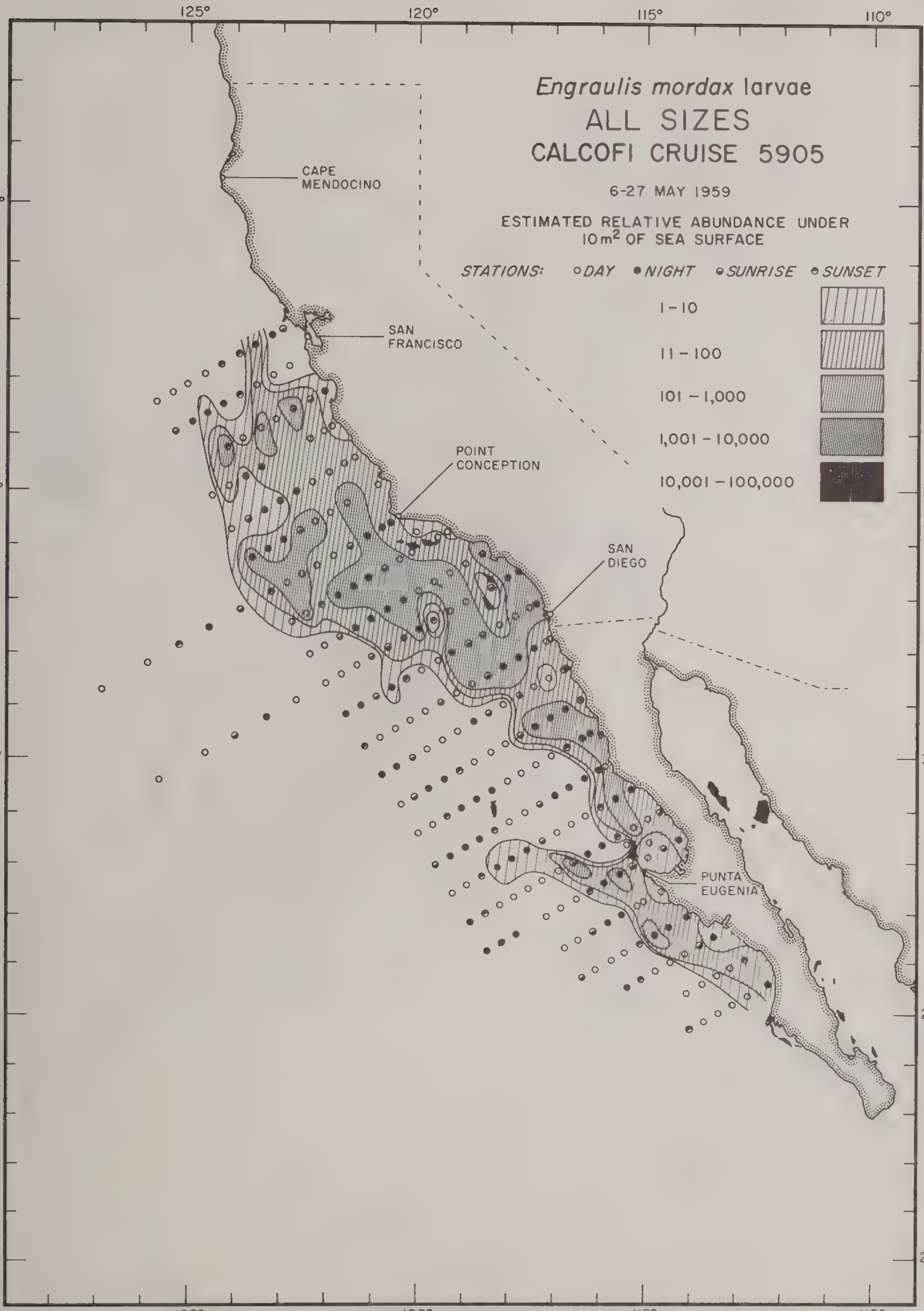
5904


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5905
6-27 MAY 1959
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

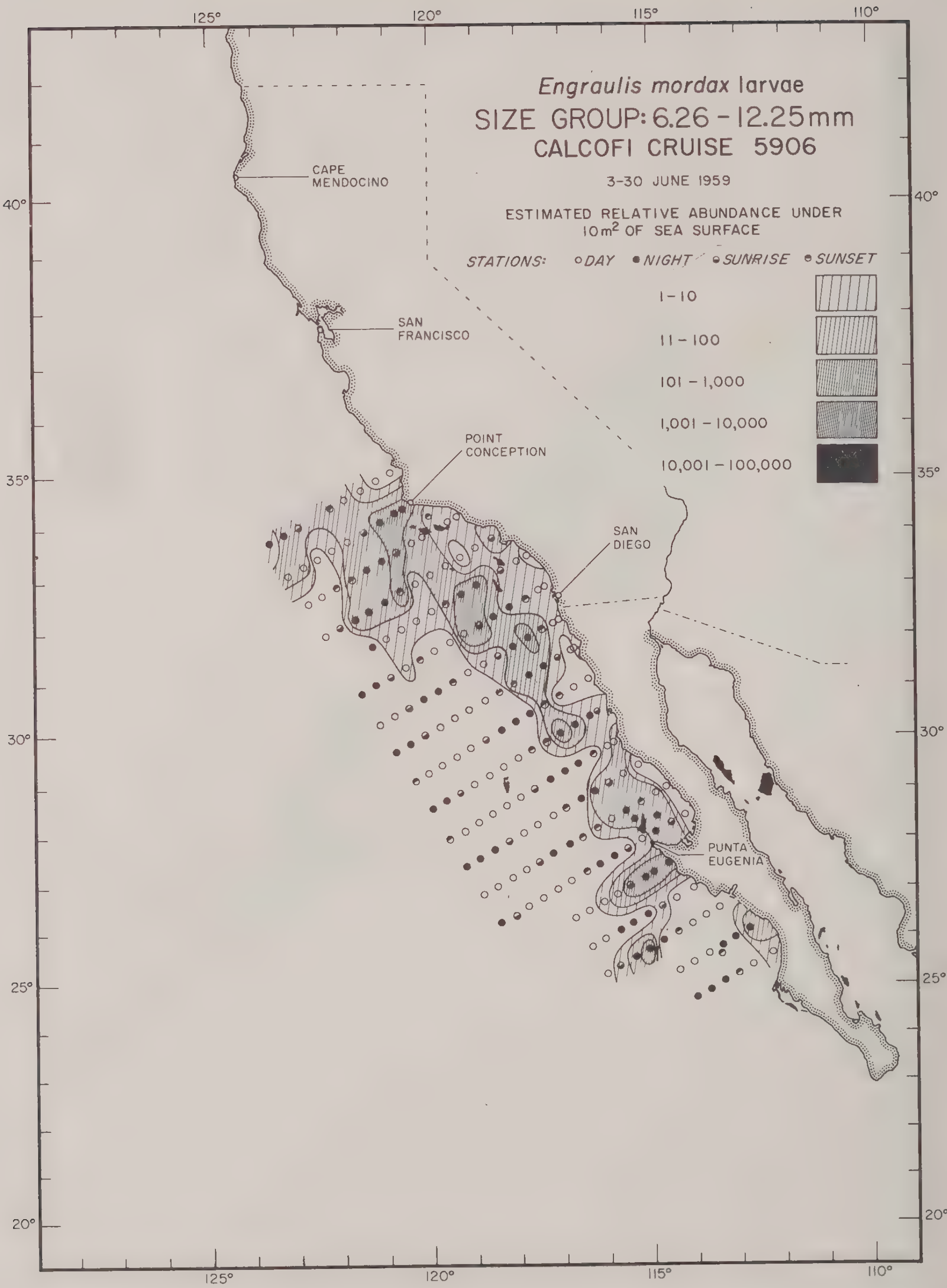
Size Group: 6.26-12.25mm

5905


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5905
6-27 MAY 1959
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

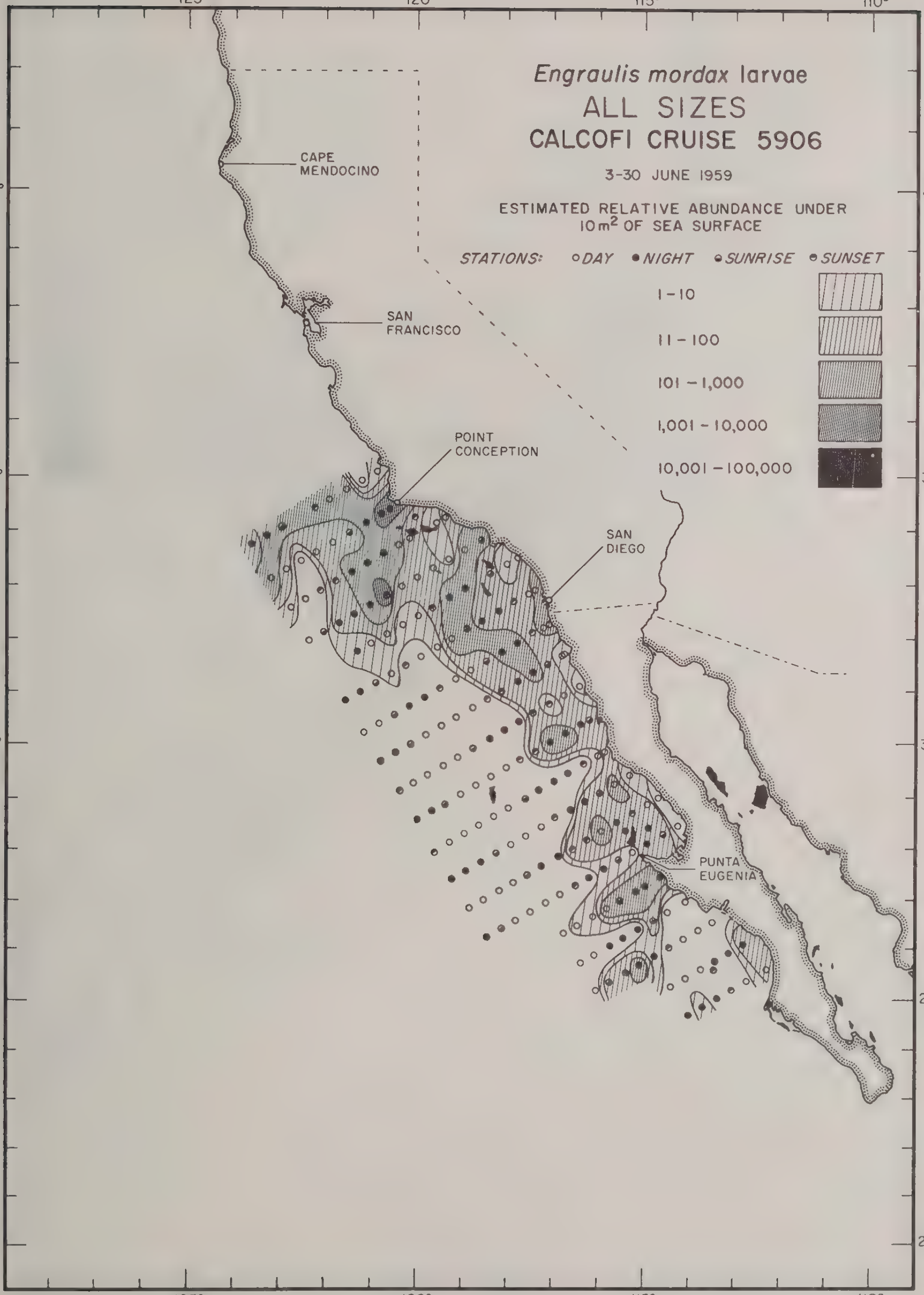
All Sizes
5905


125°
120°
115°
110°
Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5906
3-30 JUNE 1959
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◐SUNRISE ◑SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
40°
35°
30°
25°
20°

Engraulis mordax larvae

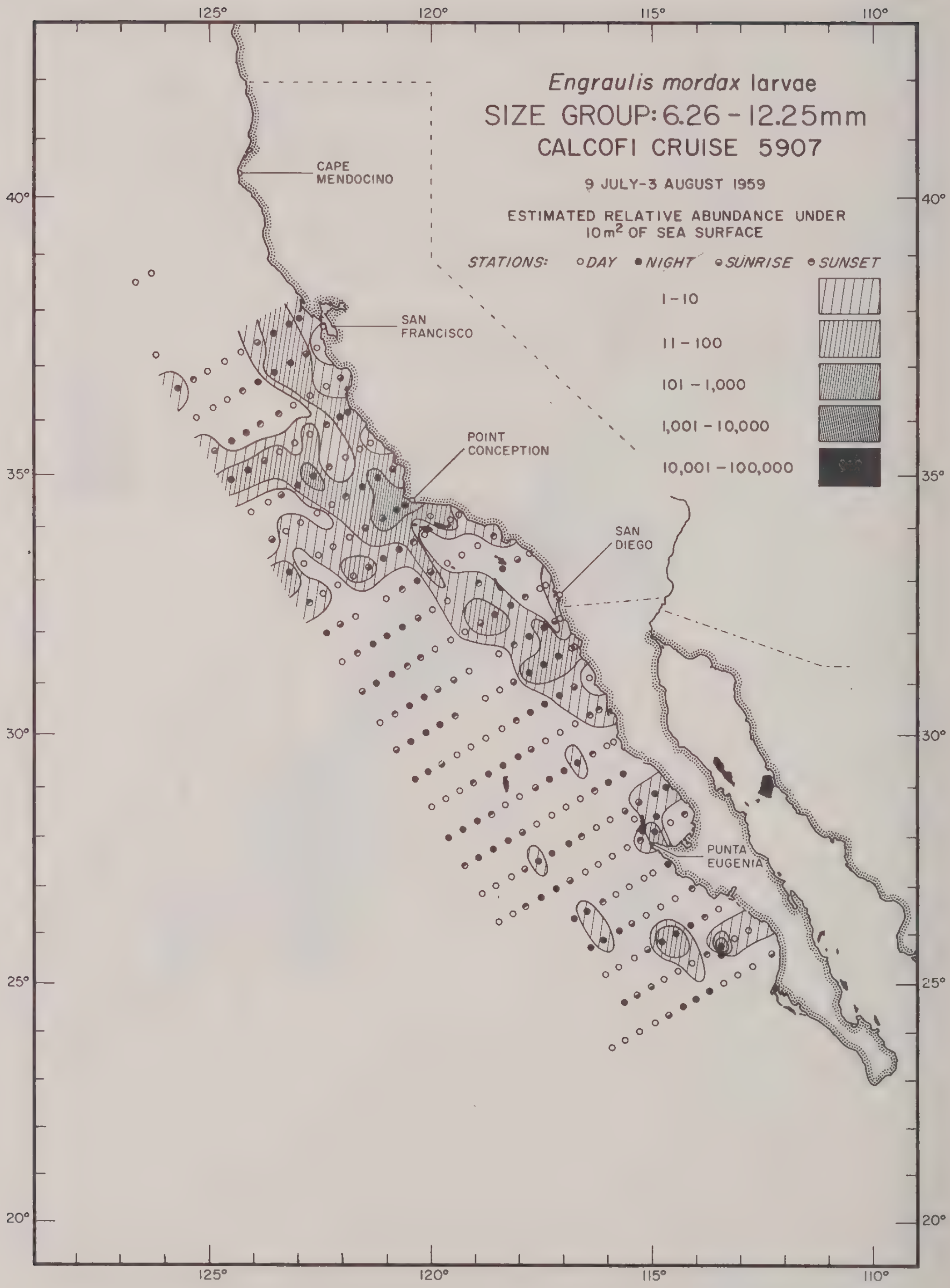
Size Group: 6.26-12.25mm

5906


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5906
3-30 JUNE 1959
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

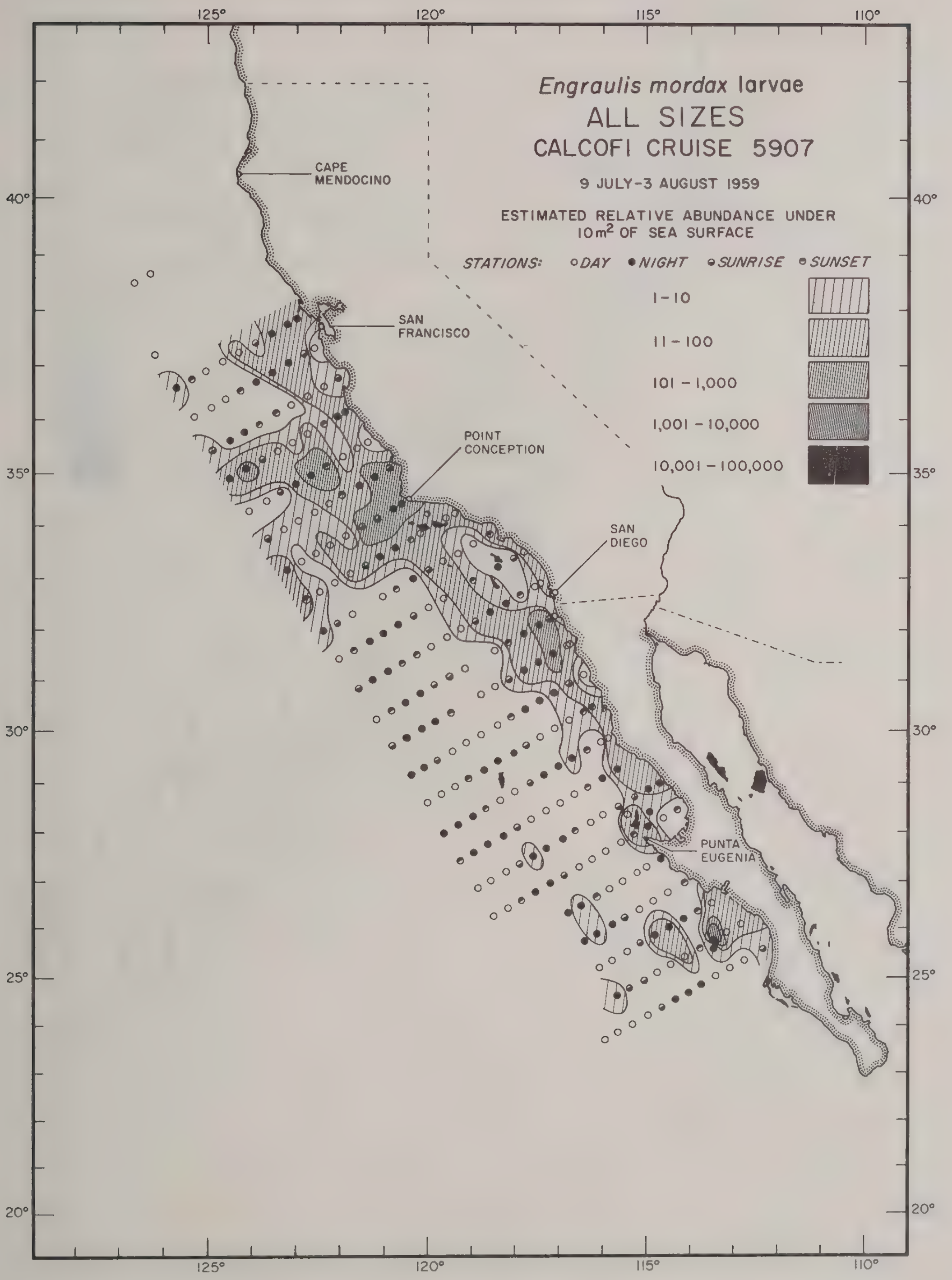
All Sizes
5906


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5907
9 JULY-3 AUGUST 1959
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

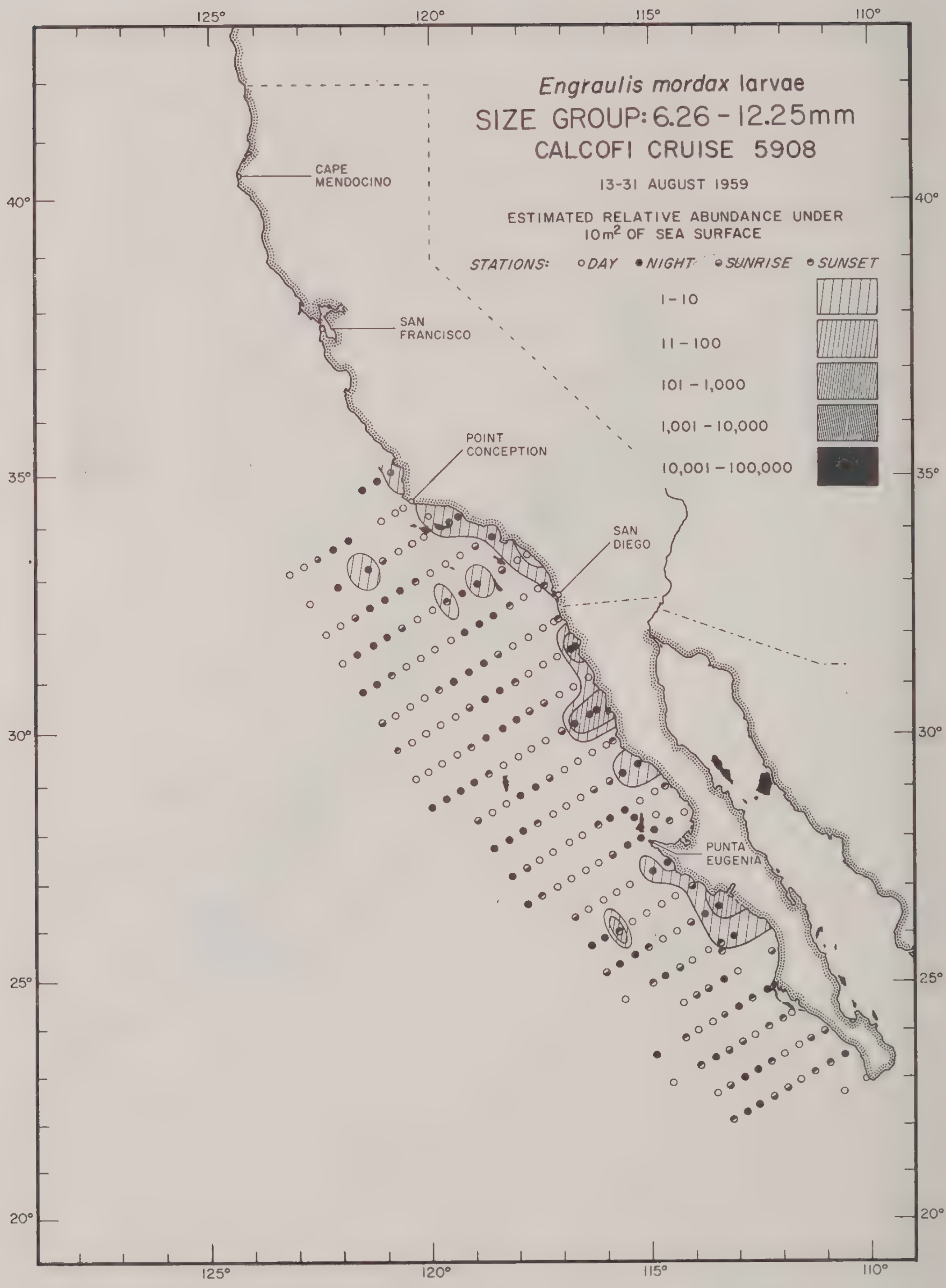
5907


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5907
9 JULY-3 AUGUST 1959
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

All Sizes

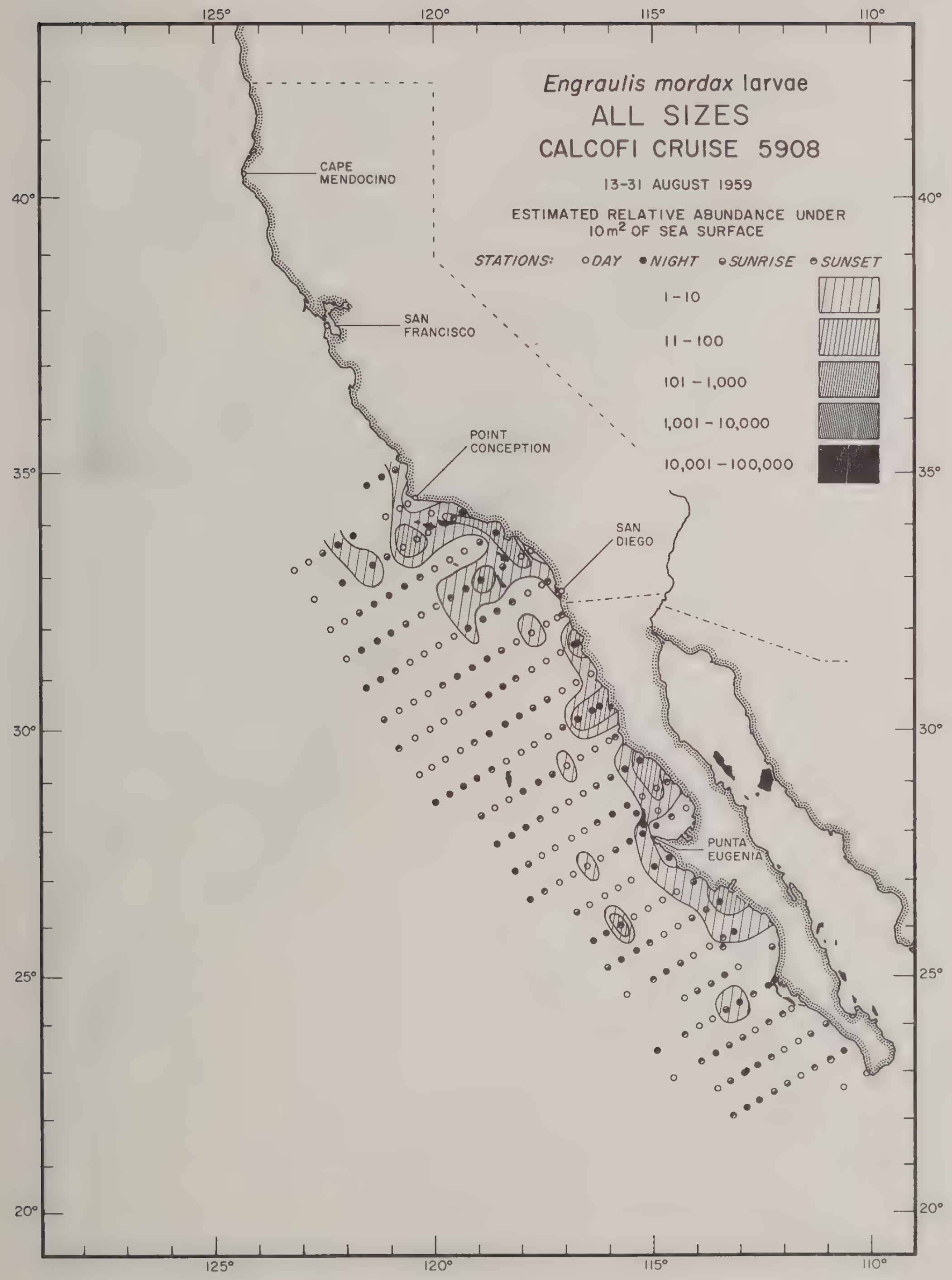
5907


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5908
13-31 AUGUST 1959
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ *DAY* ● *NIGHT* ◐ *SUNRISE* ◑ *SUNSET*
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

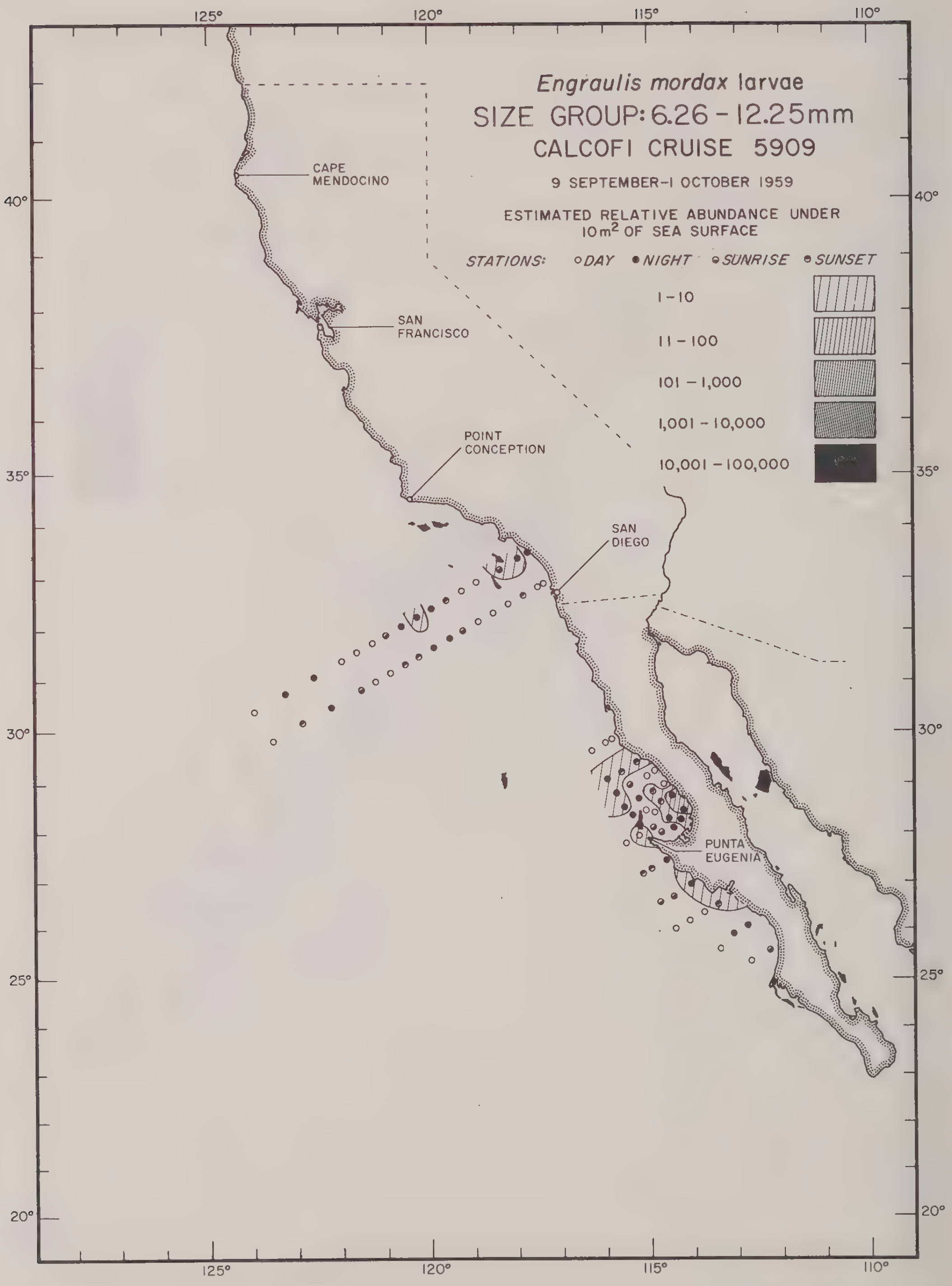
5908


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5908
13-31 AUGUST 1959
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◉ SUNRISE ◉ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

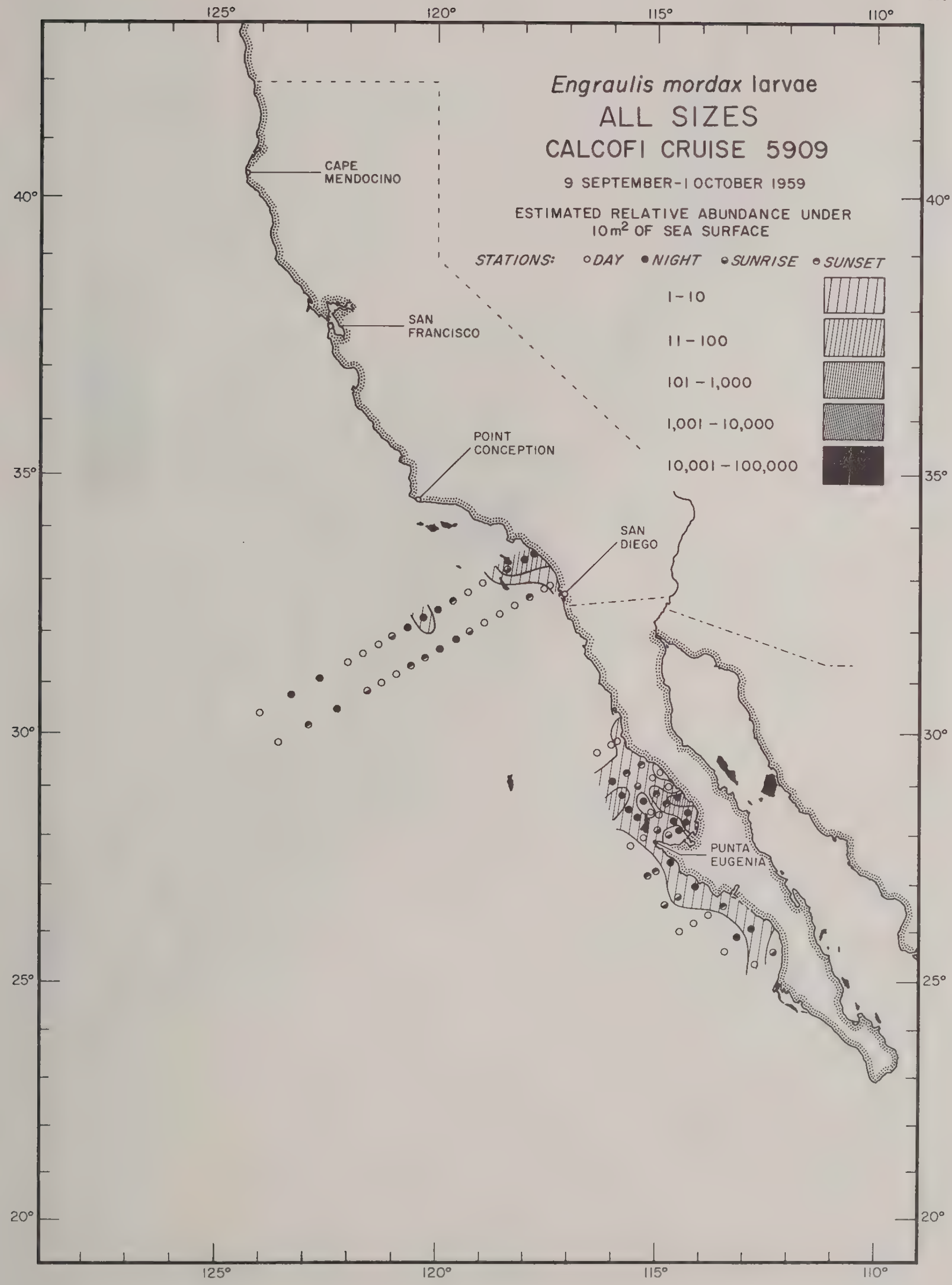
5908


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5909
9 SEPTEMBER-1 OCTOBER 1959
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◉SUNRISE ◉SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

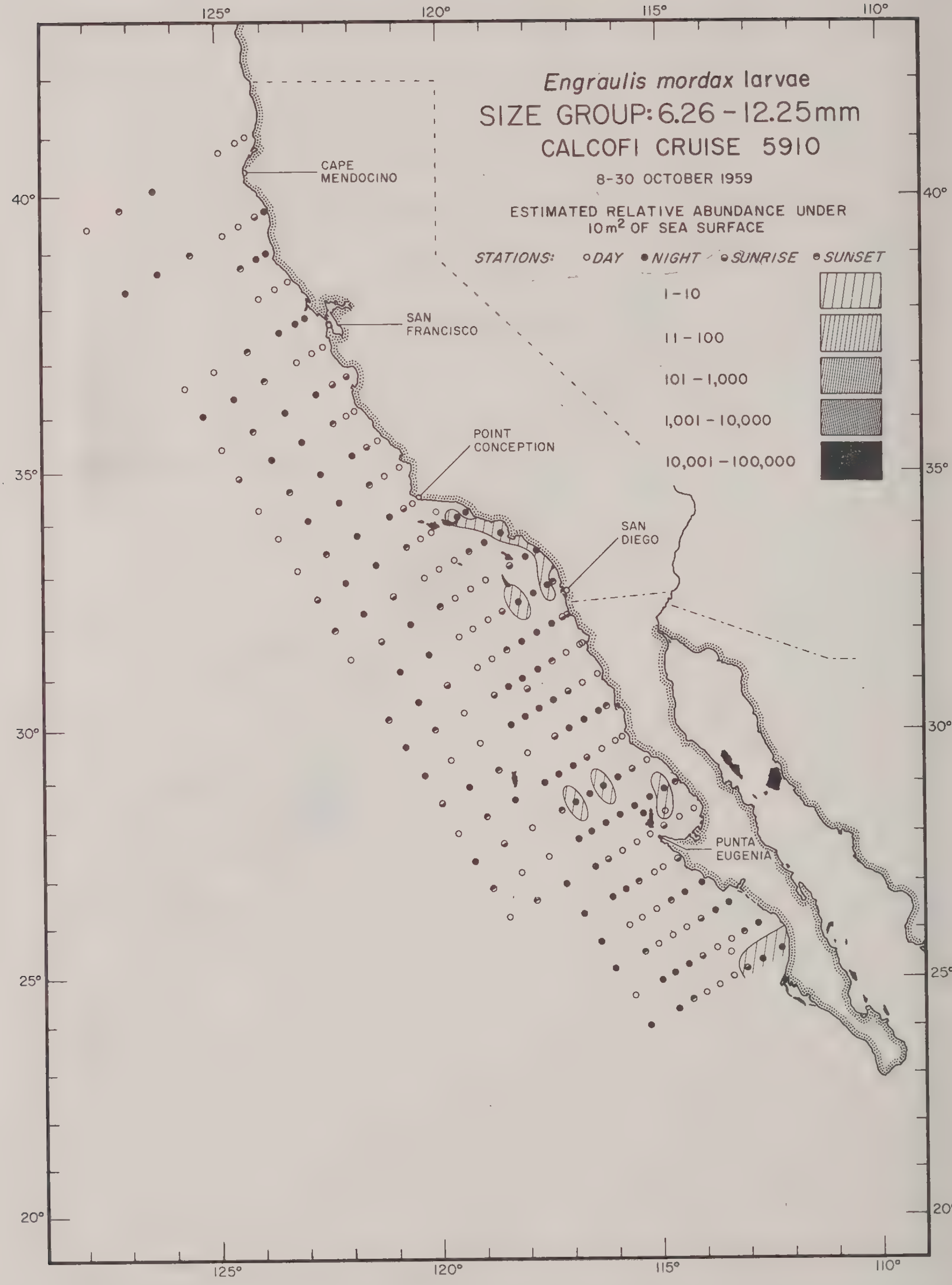
5909


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5909
9 SEPTEMBER-1 OCTOBER 1959
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

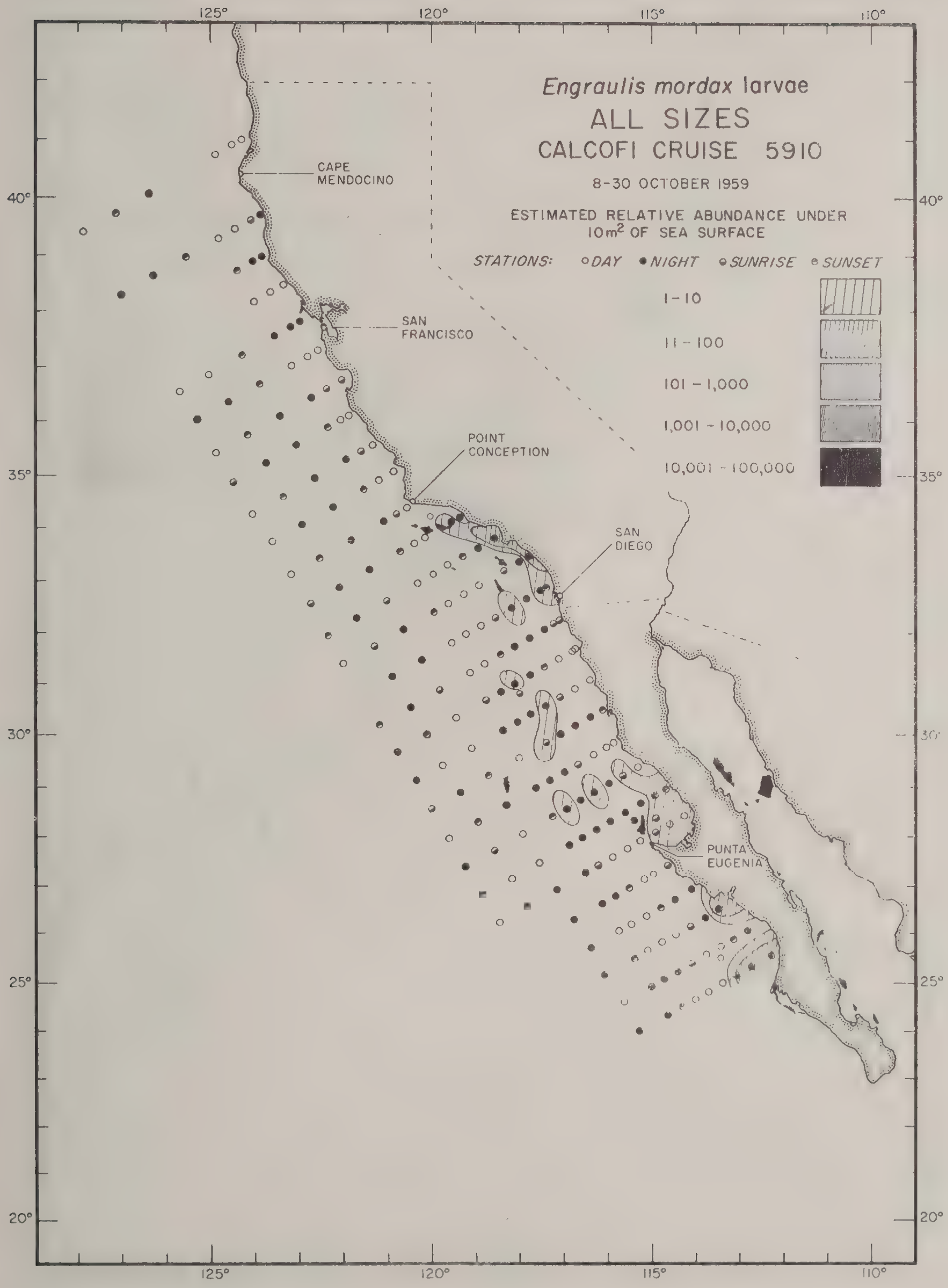
5909


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5910
8-30 OCTOBER 1959
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

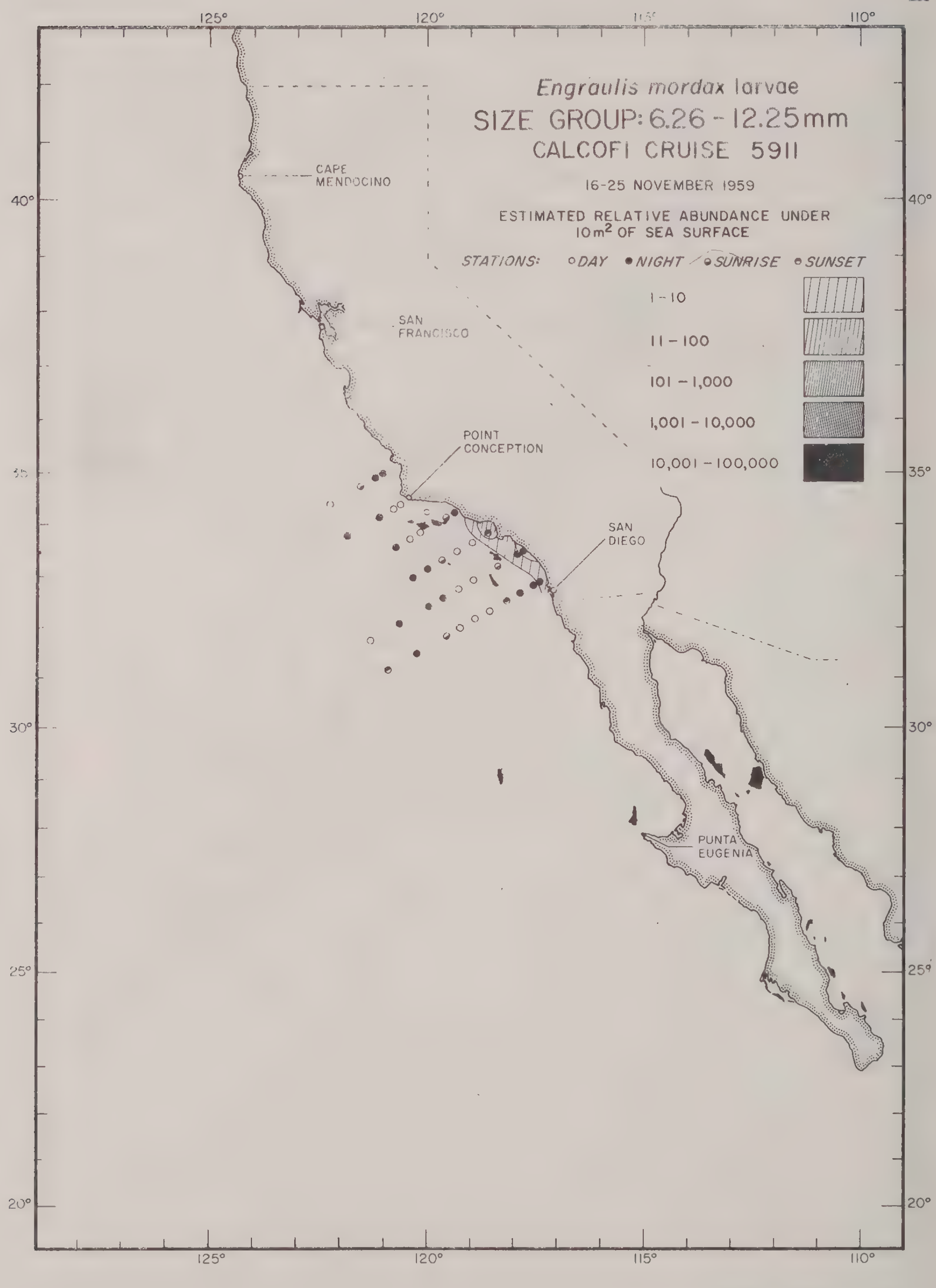
5910


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5910
8-30 OCTOBER 1959
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

5910

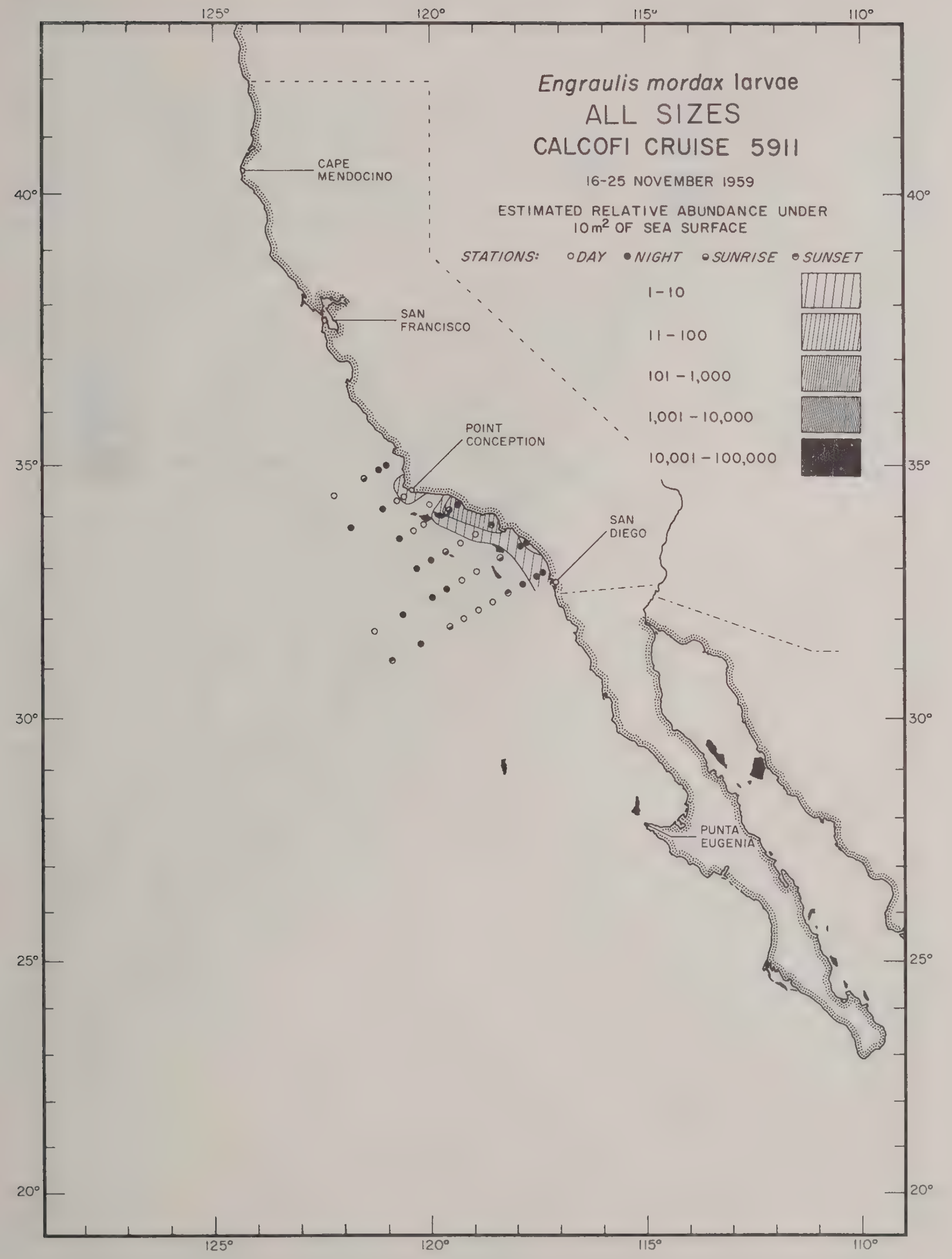


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 5911
16-25 NOVEMBER 1959
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

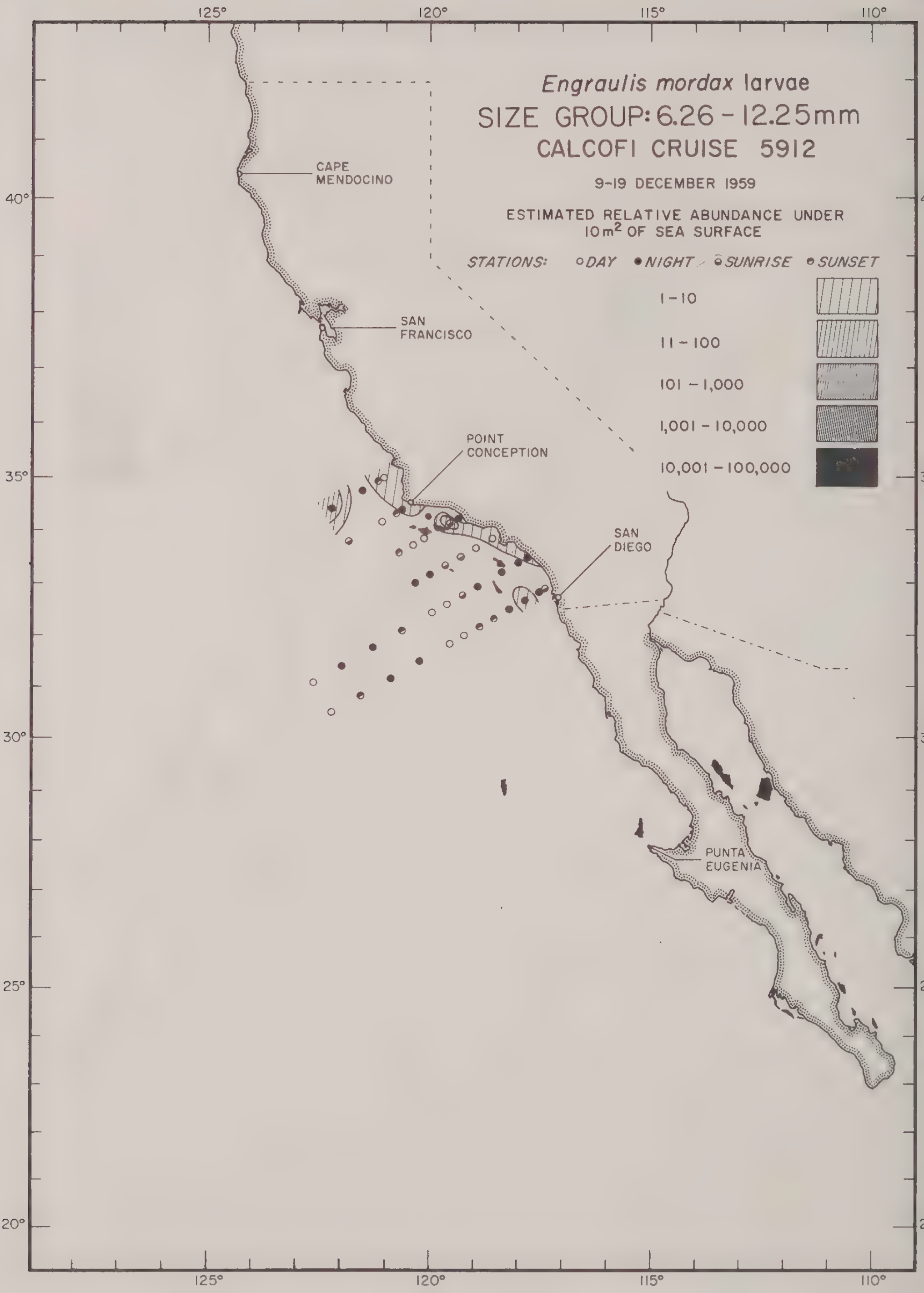
Size Group: 6.26-12.25 mm

5911


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5911
16-25 NOVEMBER 1959
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT SUNRISE SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

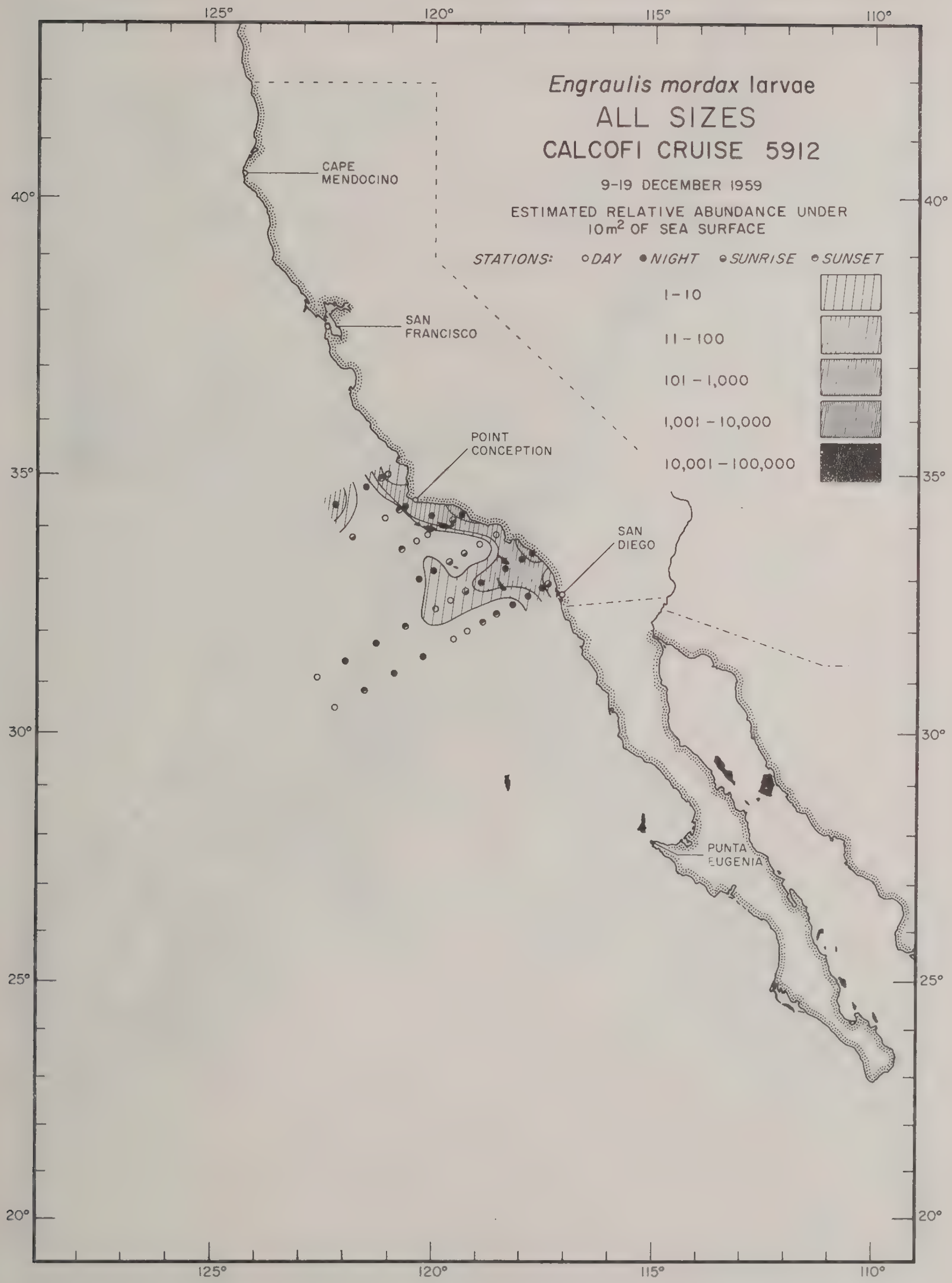
All Sizes
5911


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 5912
9-19 DECEMBER 1959
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

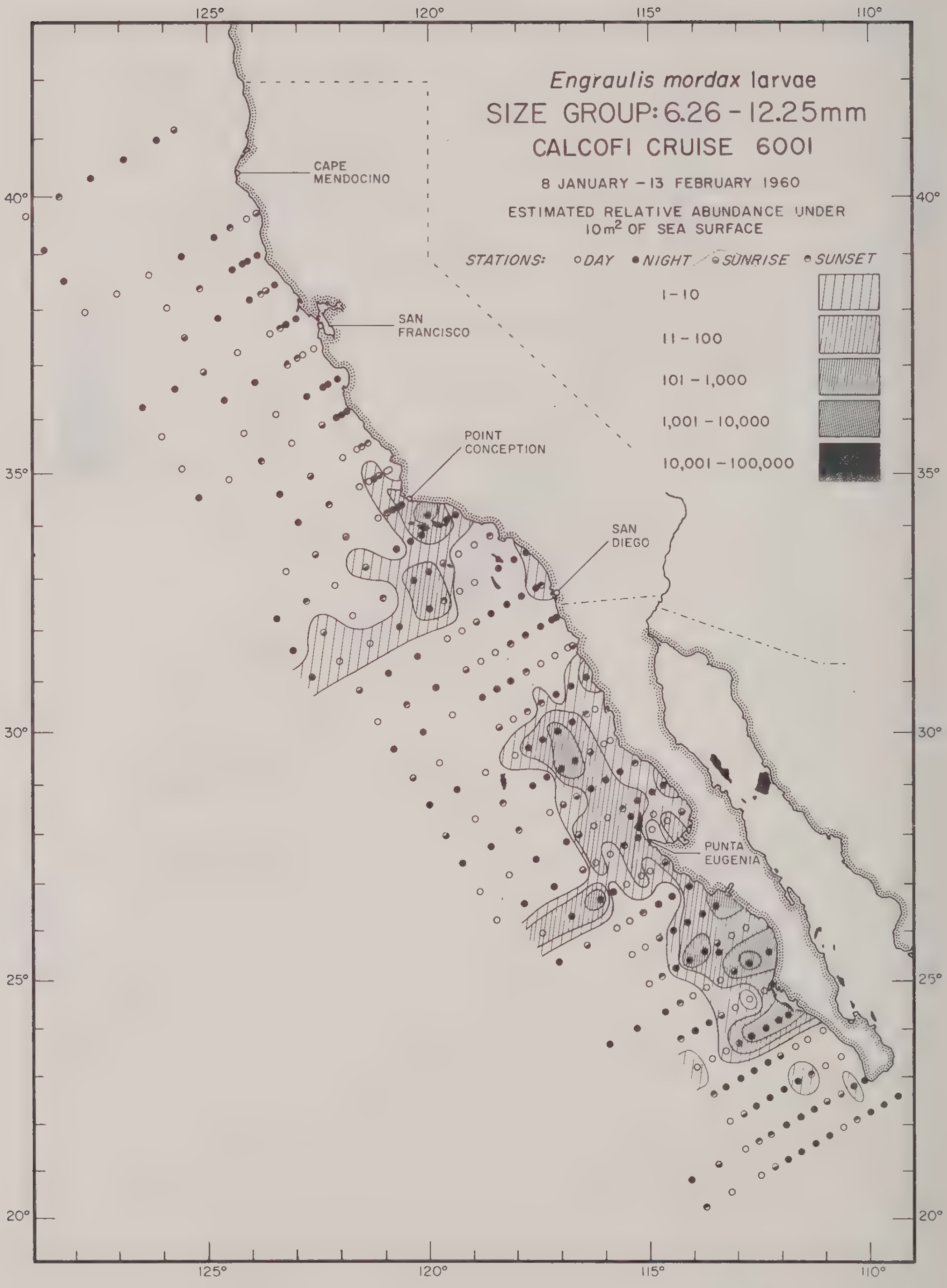
5912


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5912
9-19 DECEMBER 1959
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◉SUNRISE ◉SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

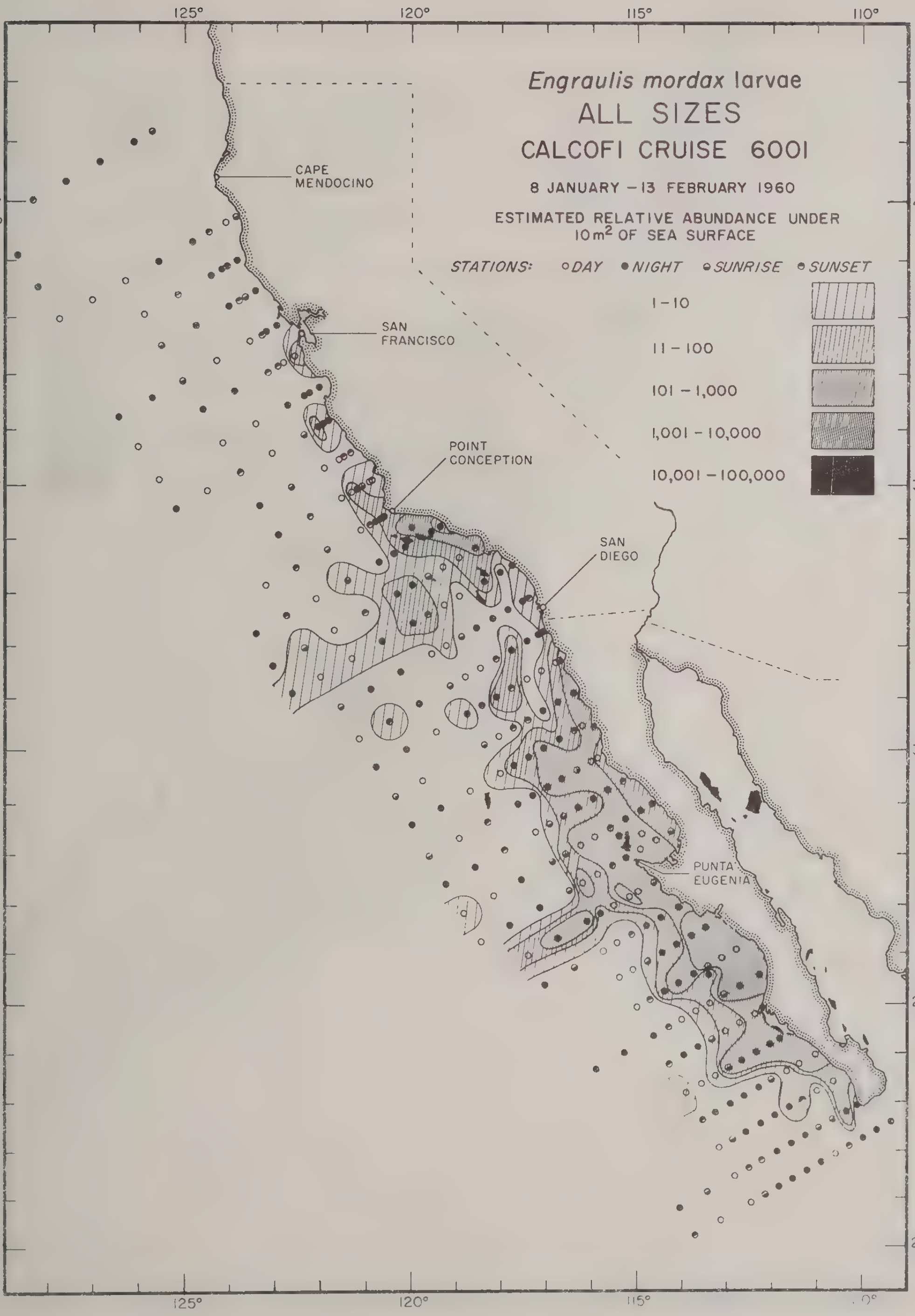
5912


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 6001
8 JANUARY - 13 FEBRUARY 1960
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

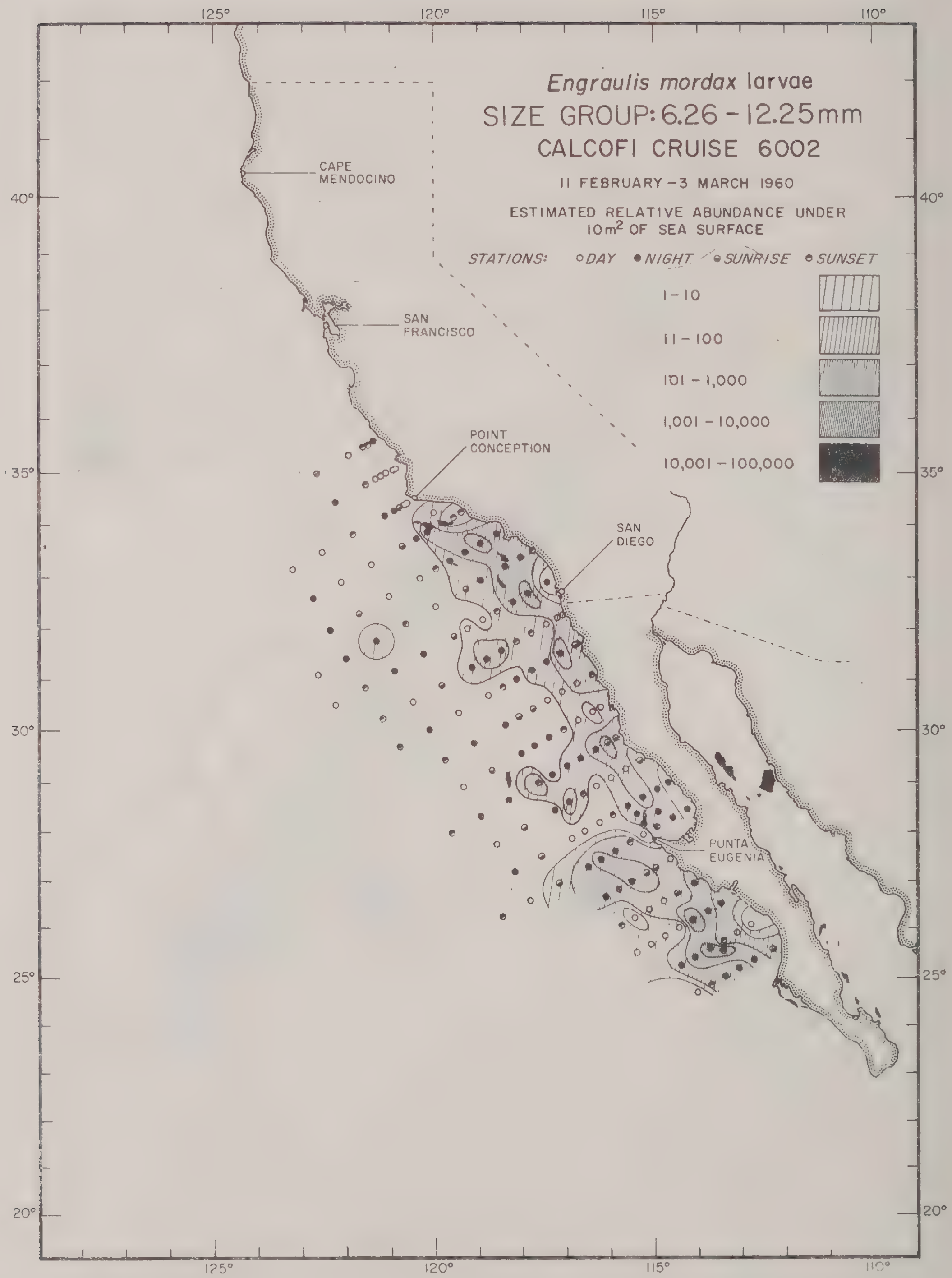
6001


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6001
8 JANUARY – 13 FEBRUARY 1960
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

All Sizes

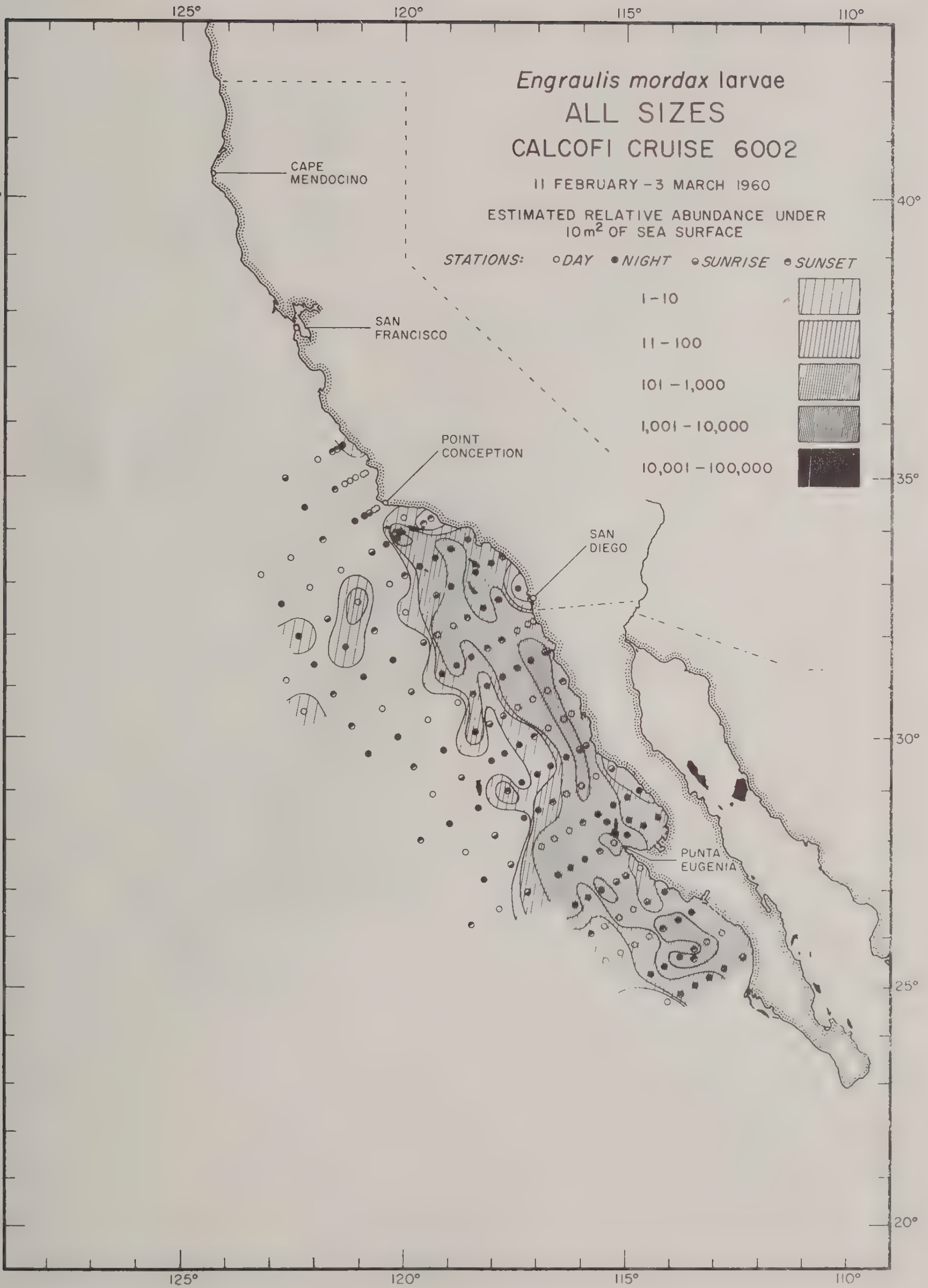
6001


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 6002
11 FEBRUARY - 3 MARCH 1960
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

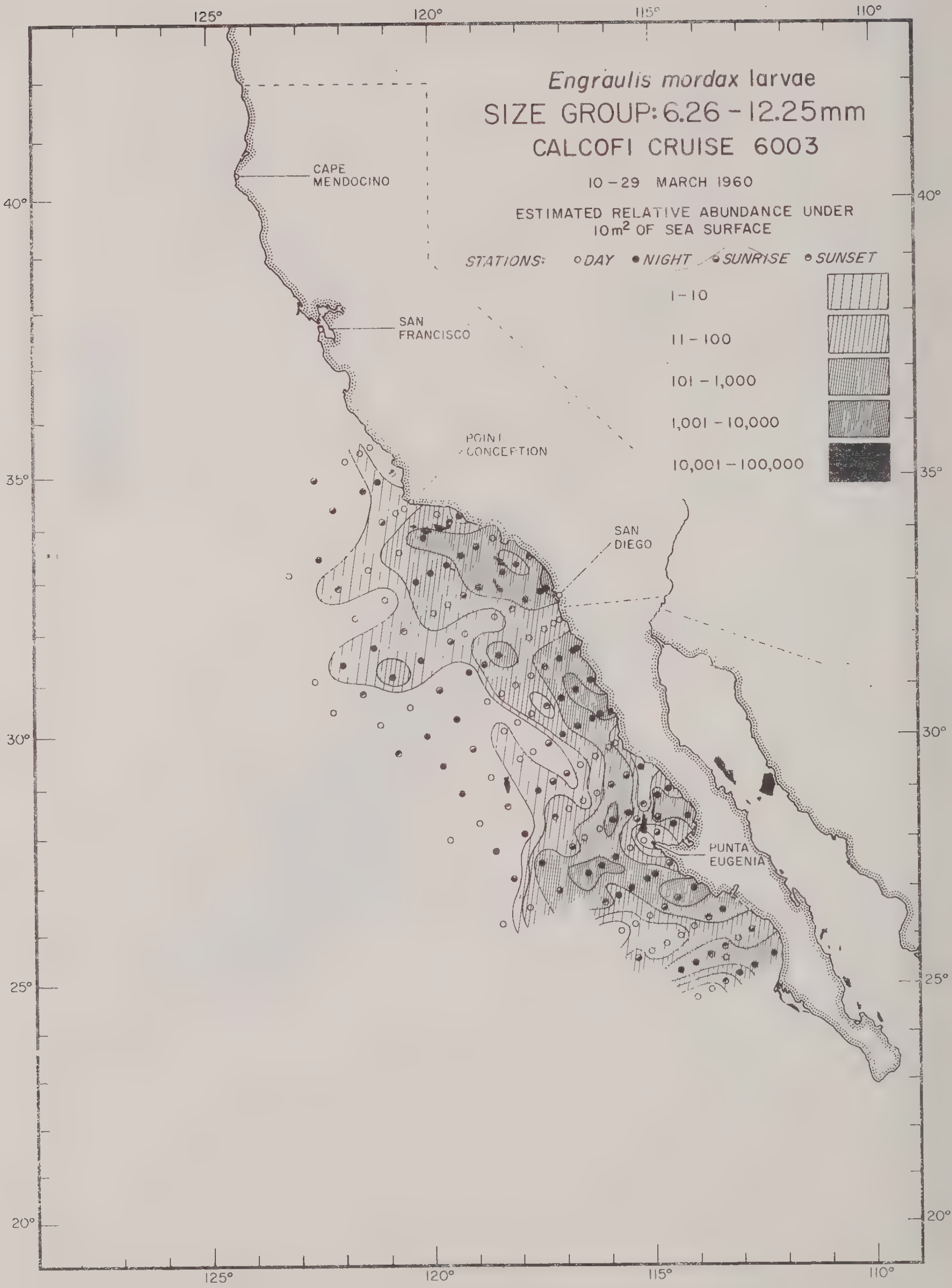
6002


125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6002
11 FEBRUARY – 3 MARCH 1960
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Engraulis mordax larvae

All Sizes

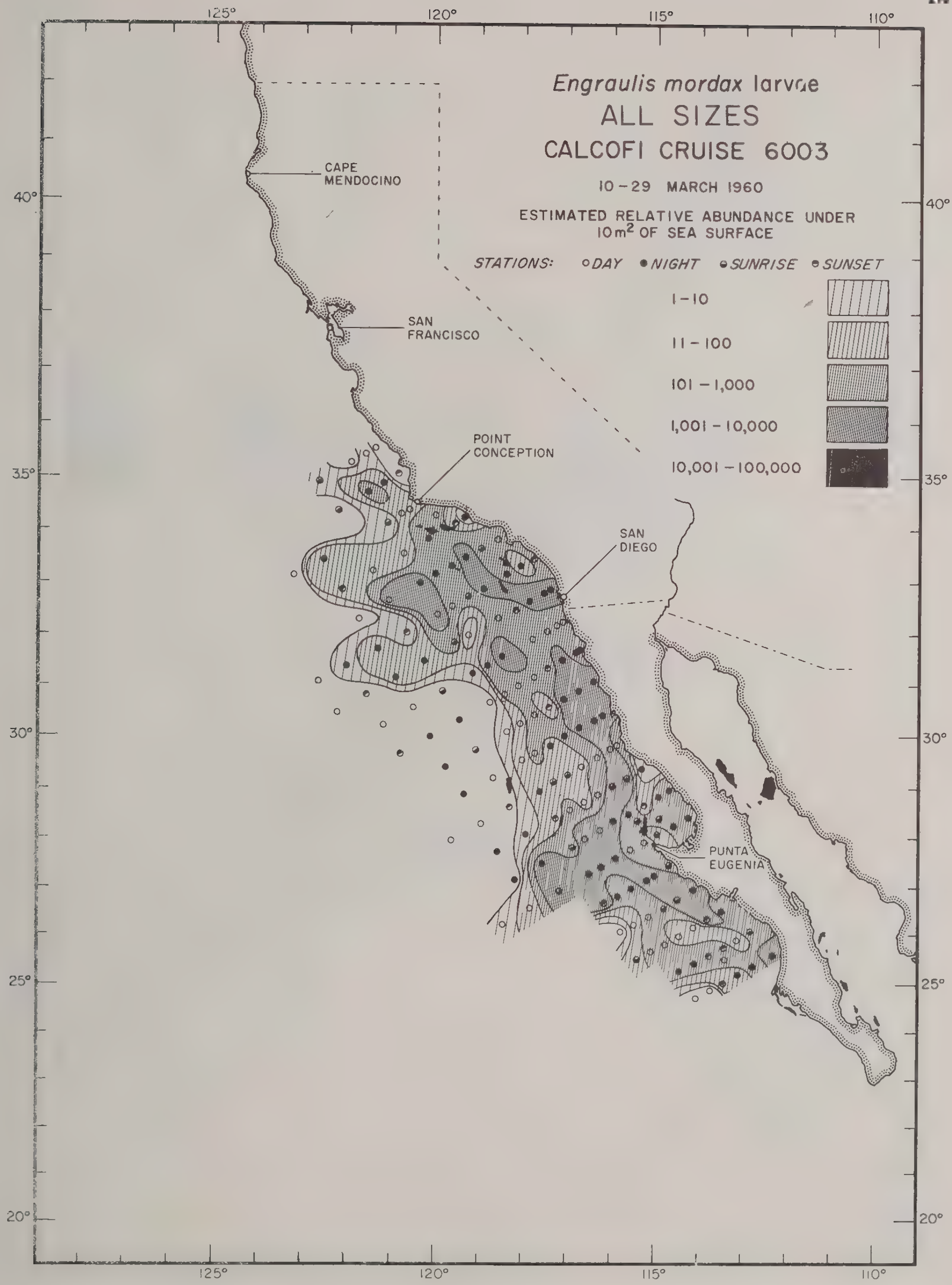
6002


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 6003
10 - 29 MARCH 1960
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

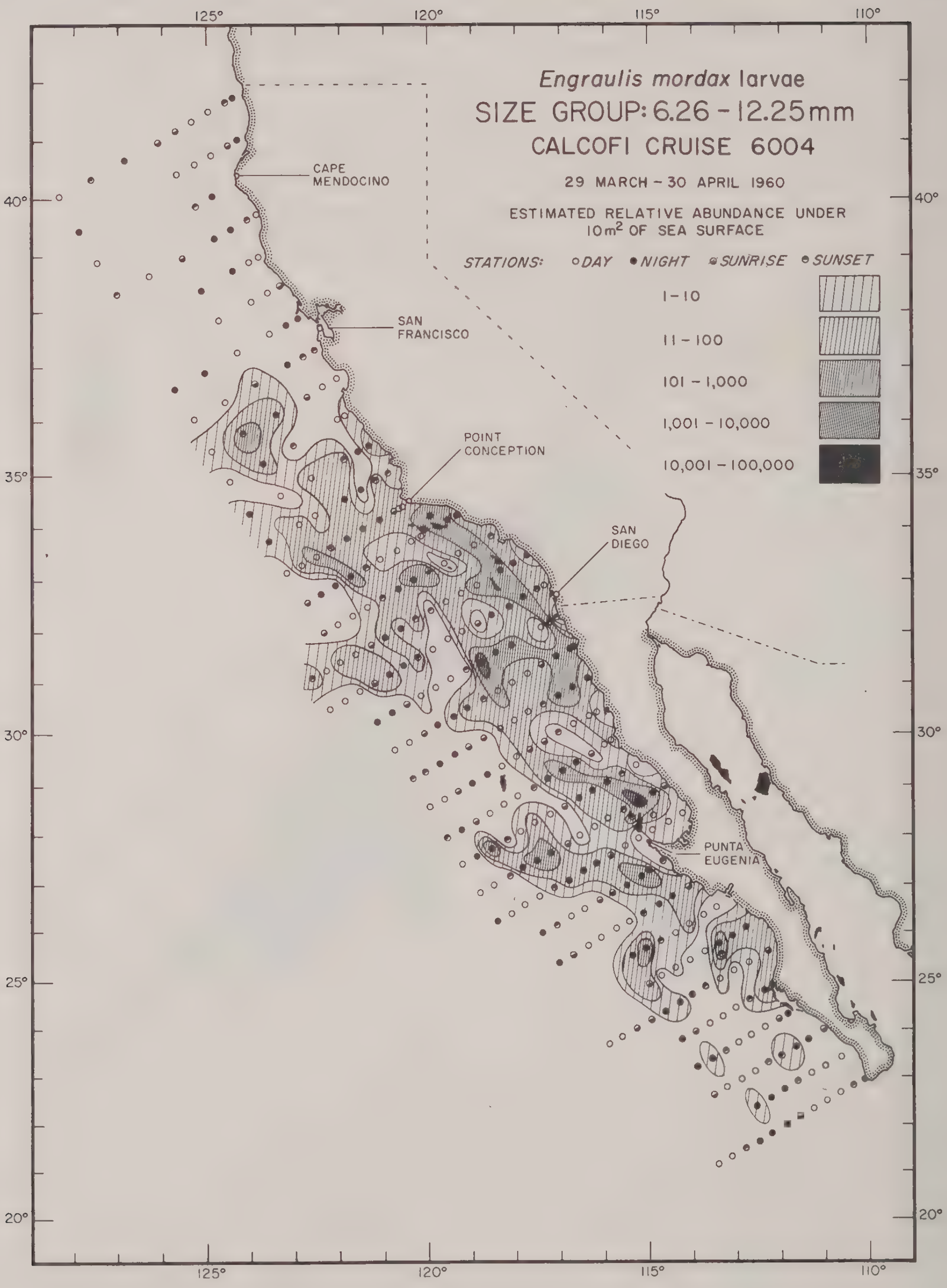
Size Group: 6.26-12.25mm

6003


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6003
10 – 29 MARCH 1960
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

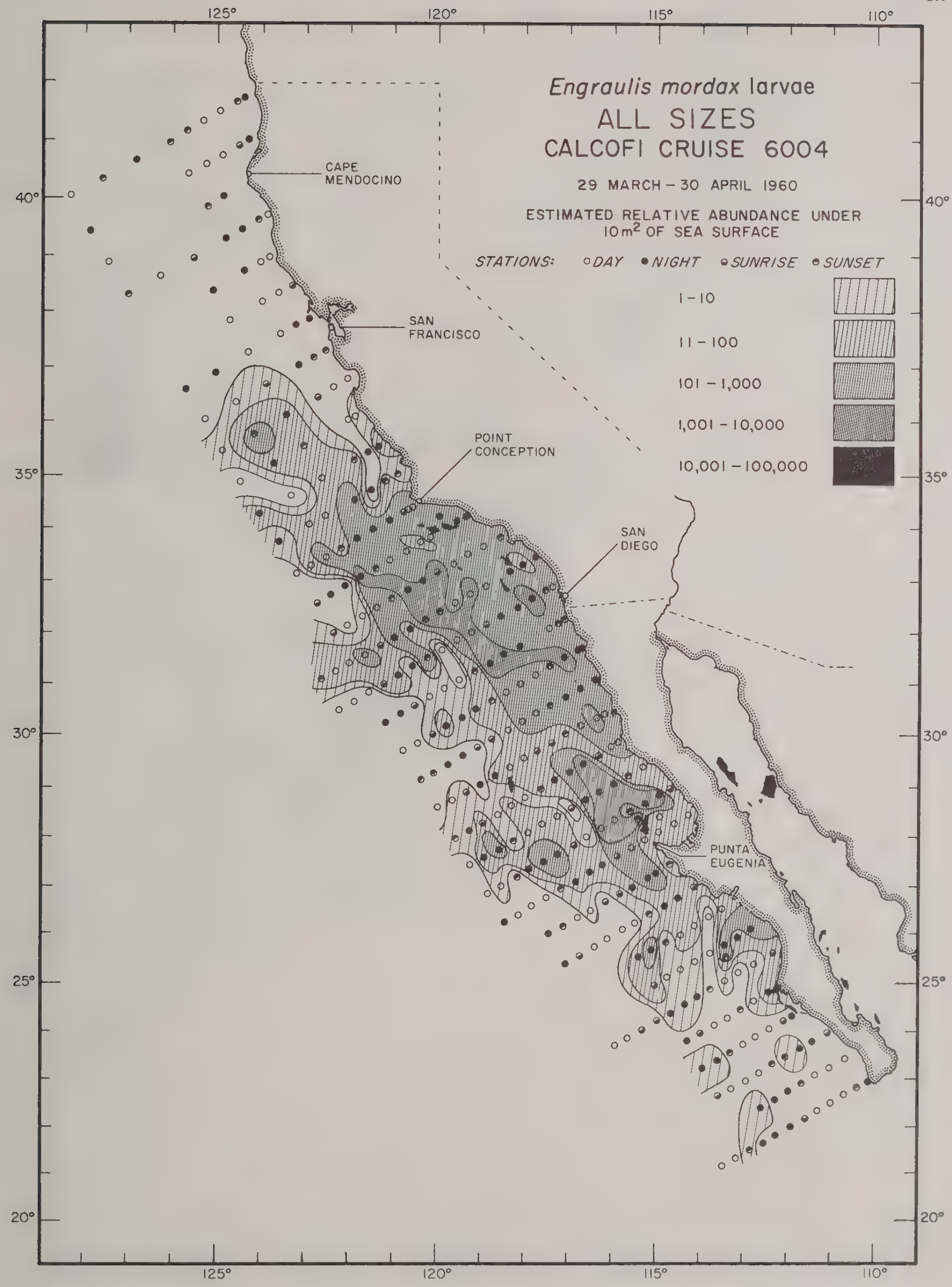
All Sizes
6003


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 6004
29 MARCH - 30 APRIL 1960
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

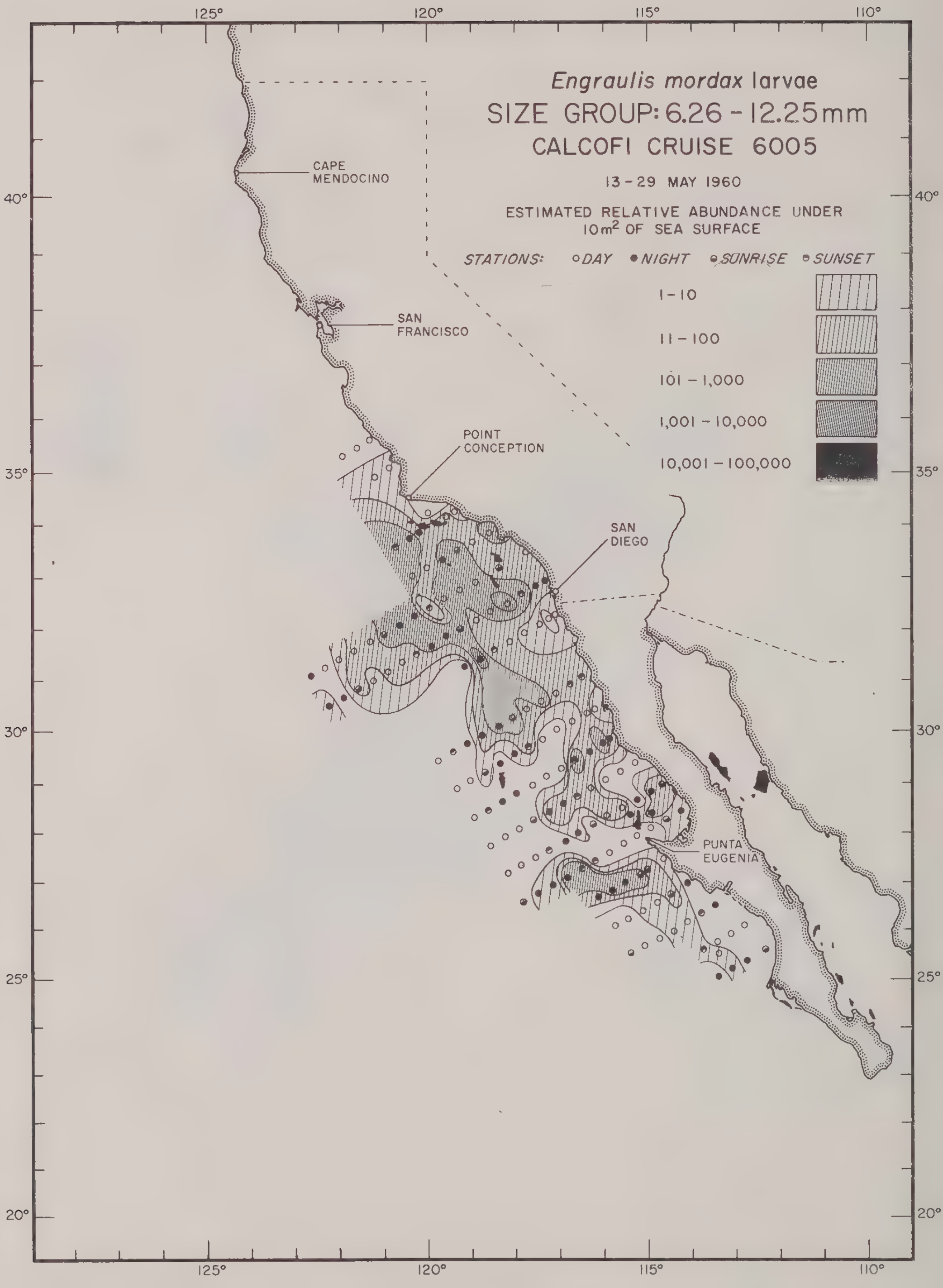
6004


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6004
29 MARCH – 30 APRIL 1960
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

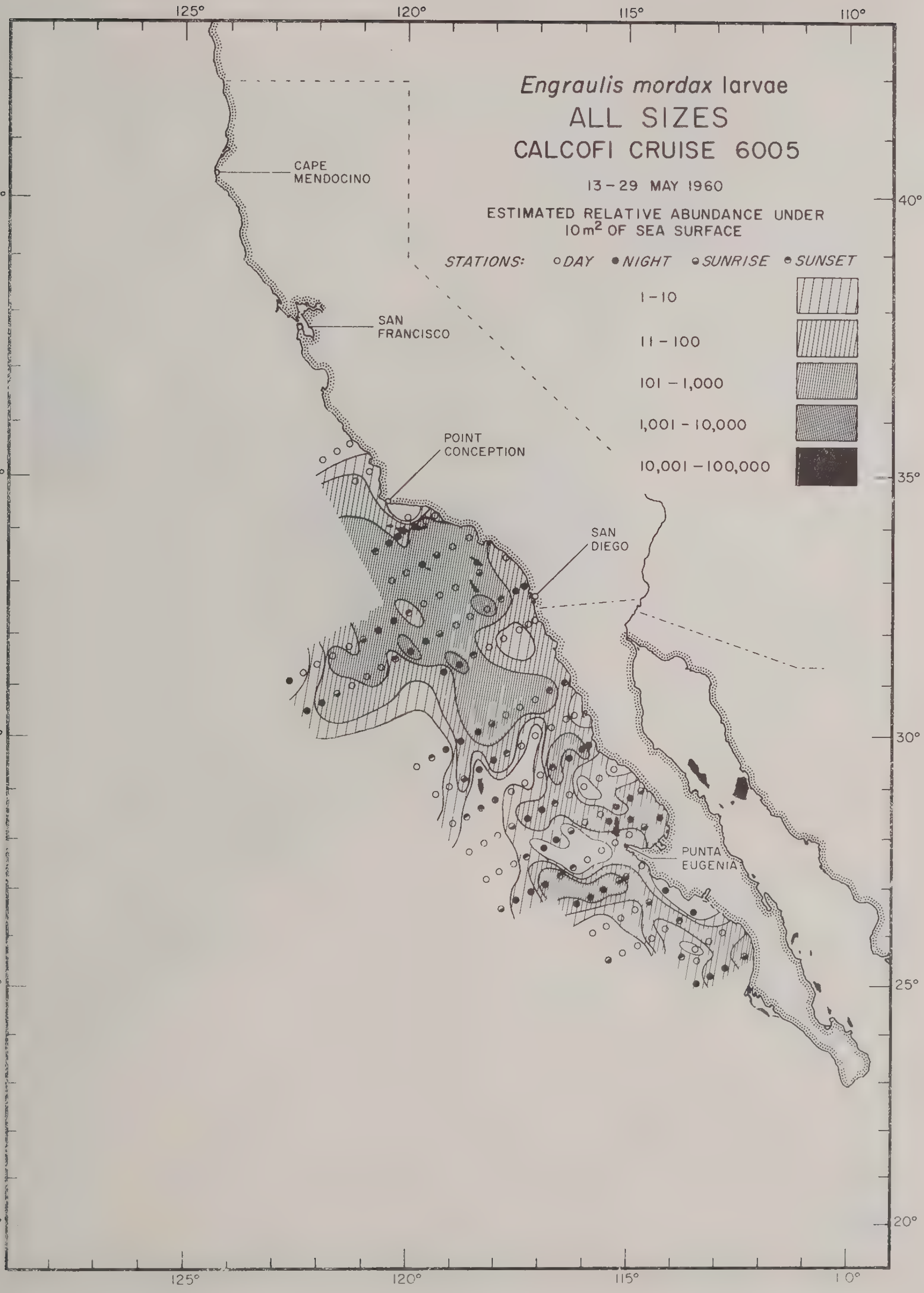
6004


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 6005
13 - 29 MAY 1960
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

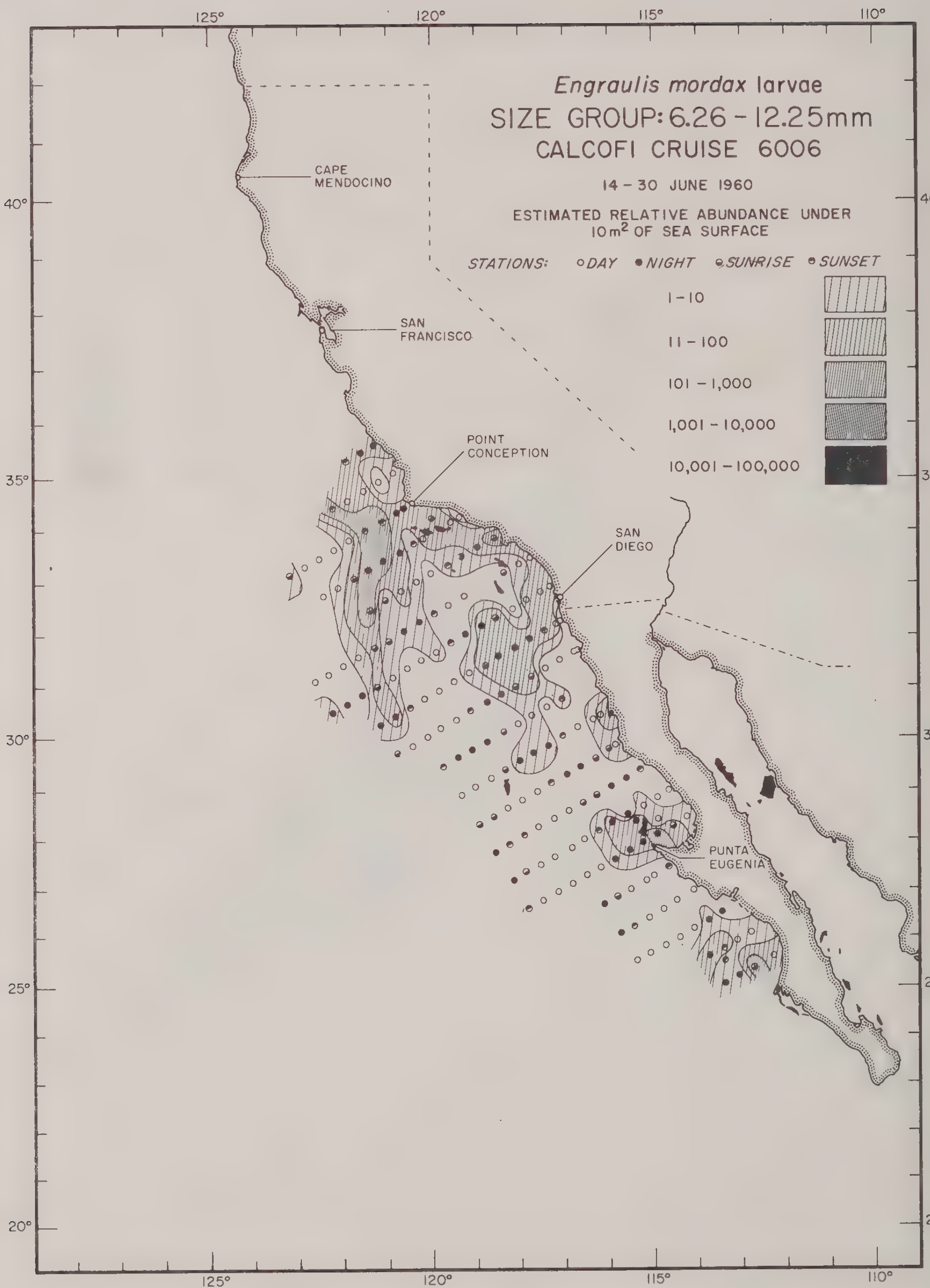
6005


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6005
13-29 MAY 1960
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

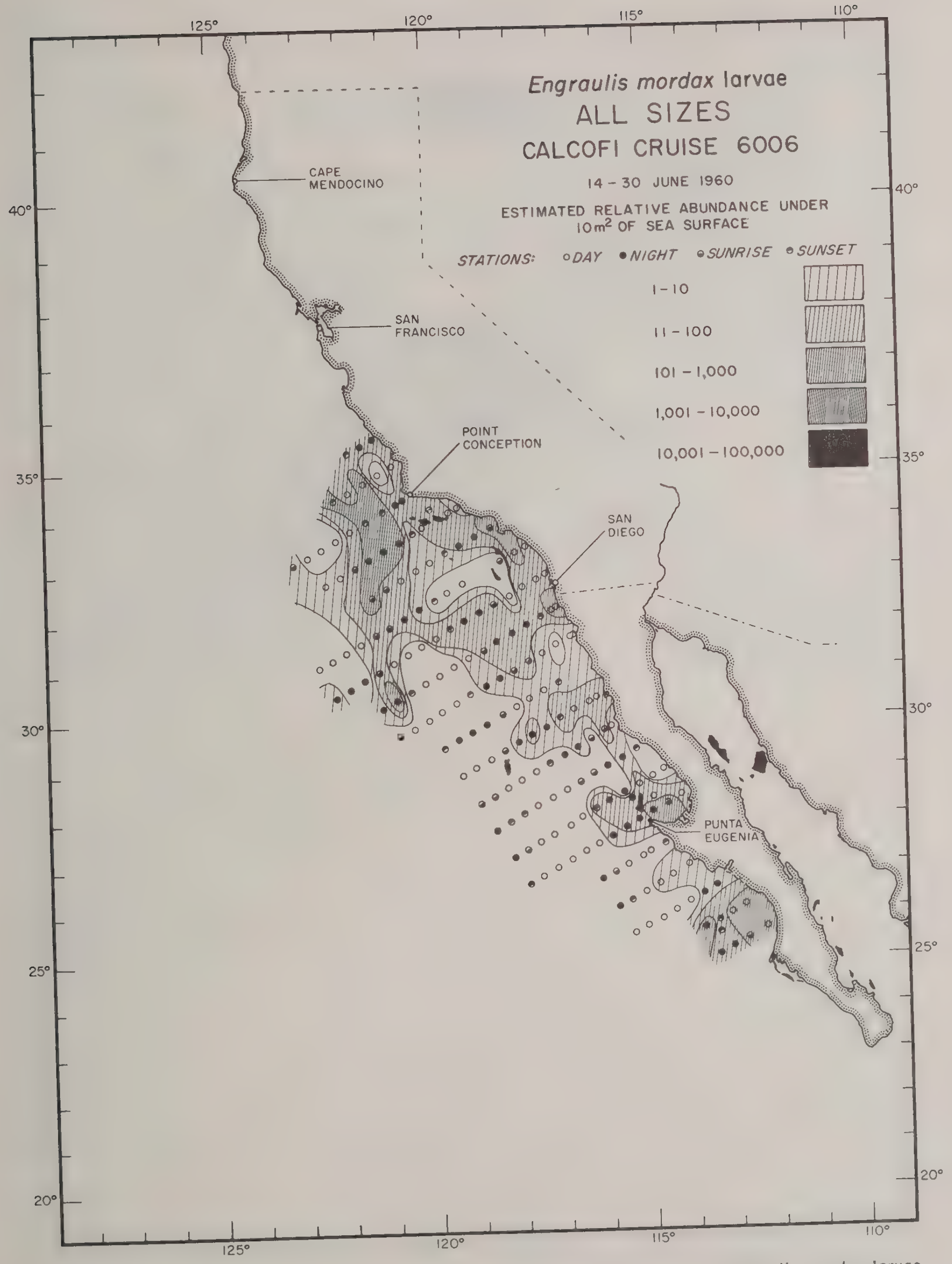
6005


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 6006
14 - 30 JUNE 1960
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

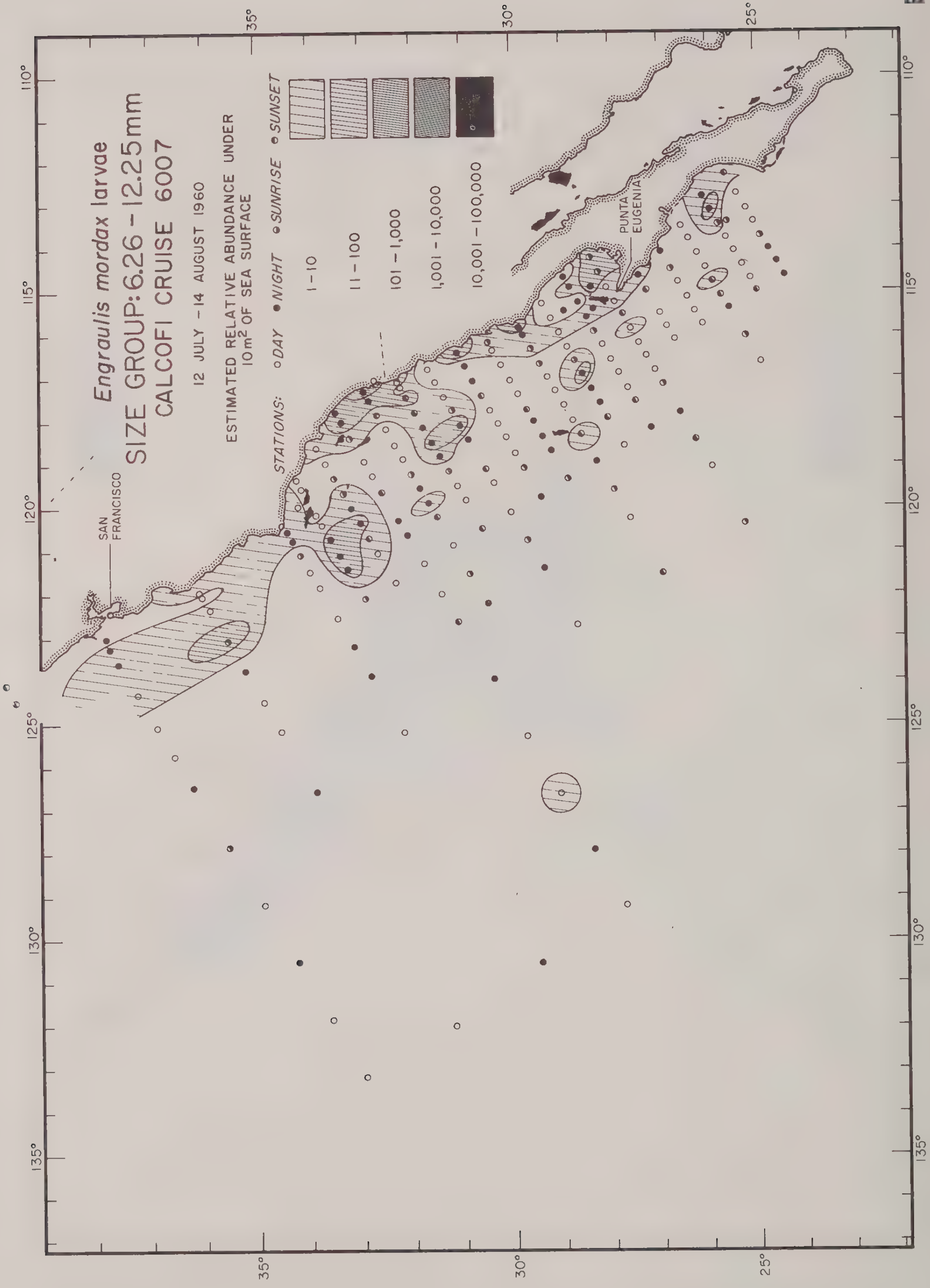
6006


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6006
14 – 30 JUNE 1960
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

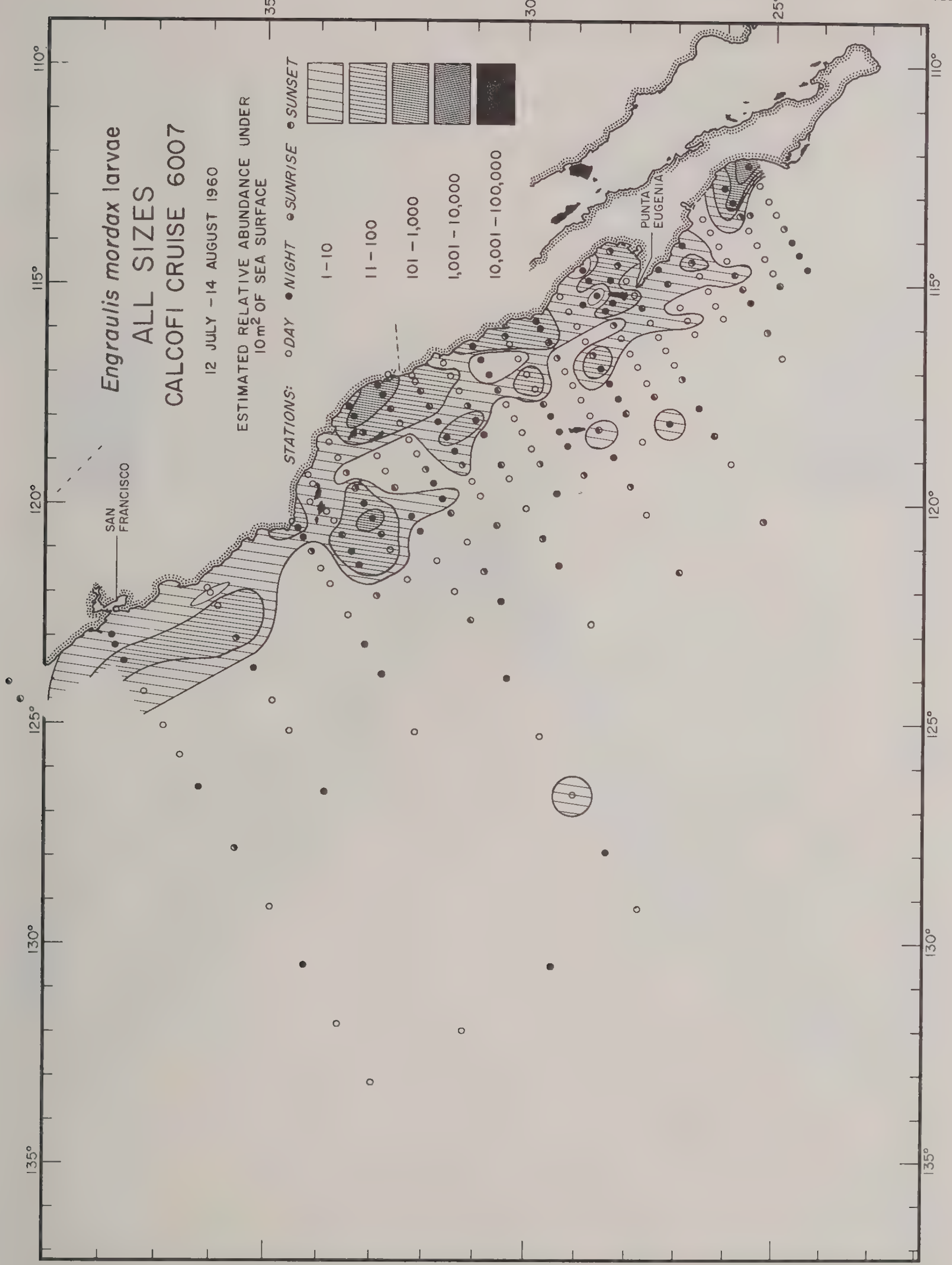
6006


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 6007
12 JULY - 14 AUGUST 1960
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
SAN FRANCISCO
PUNTA EUGENIA
35°
30°
25°
110°
115°
120°
125°
130°
135°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

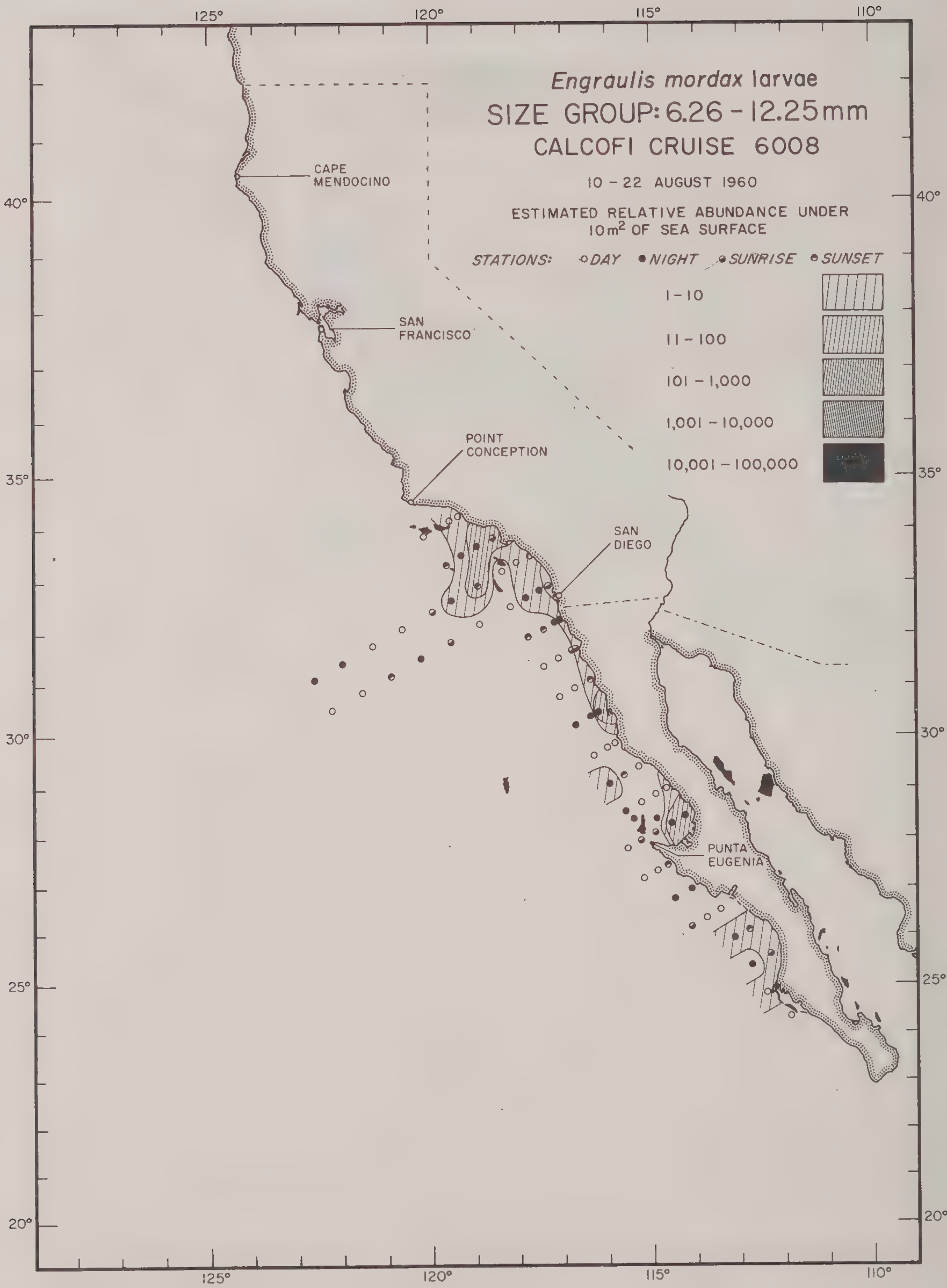
6007


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6007
12 JULY - 14 AUGUST 1960
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
SAN FRANCISCO
PUNTA EUGENIA
35°
30°
25°
110°
115°
120°
125°
130°
135°

Engraulis mordax larvae

All Sizes

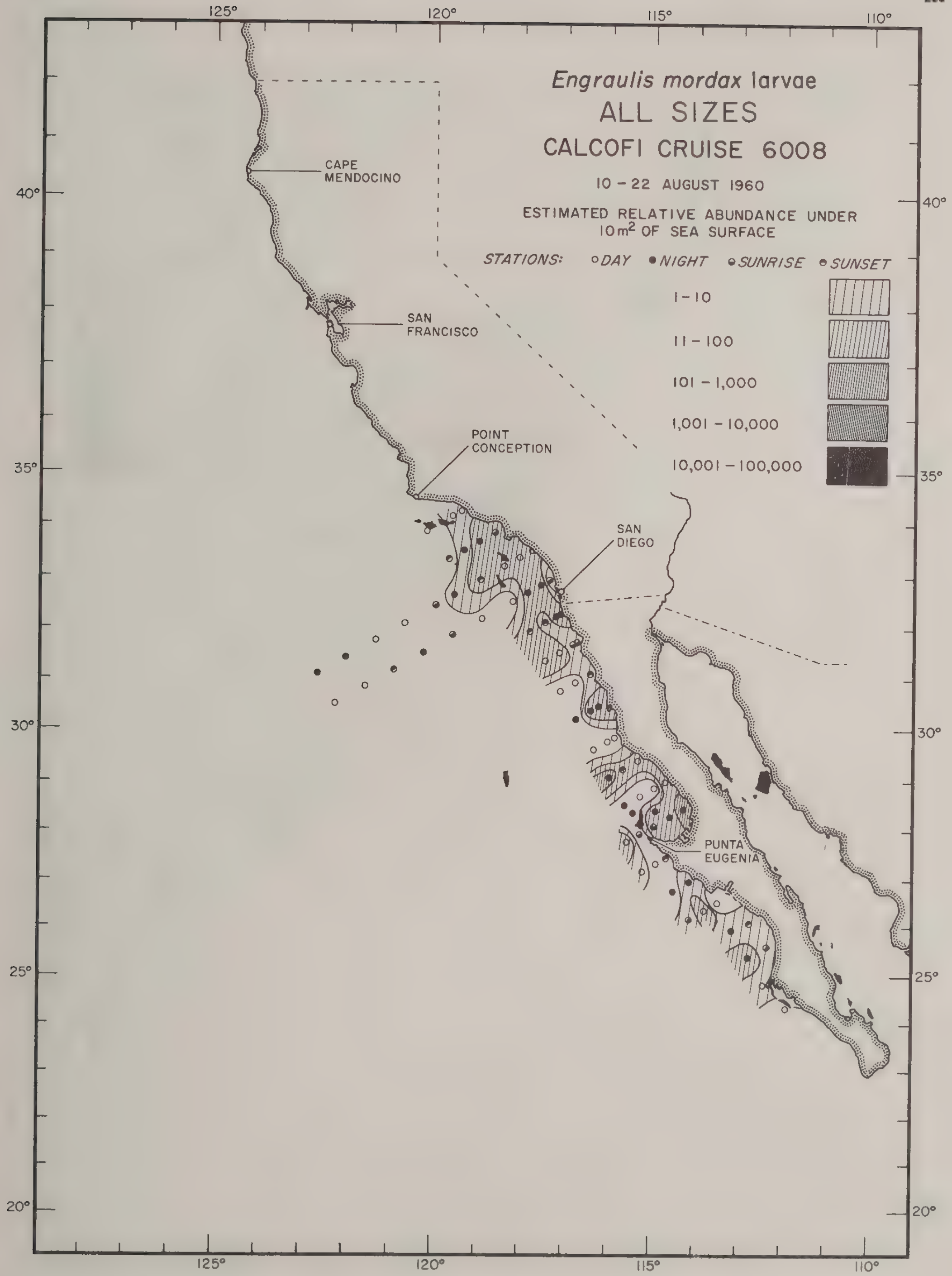
6007


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 6008
10 - 22 AUGUST 1960
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m^2 OF SEA SURFACE
STATIONS: ○ *DAY* ● *NIGHT* ◐ *SUNRISE* ◑ *SUNSET*
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

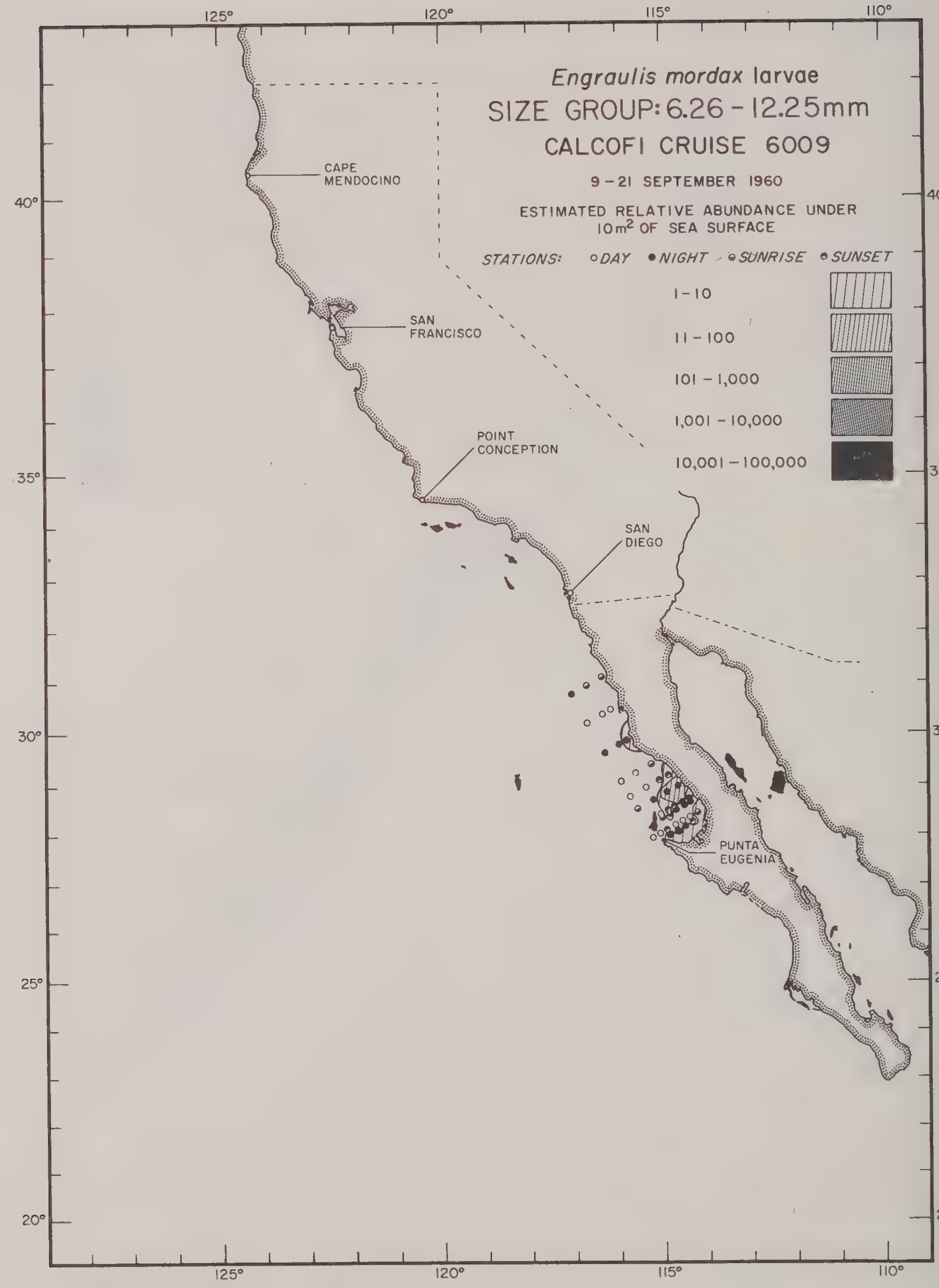
Size Group: 6.26-12.25mm

6008


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6008
10 – 22 AUGUST 1960
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

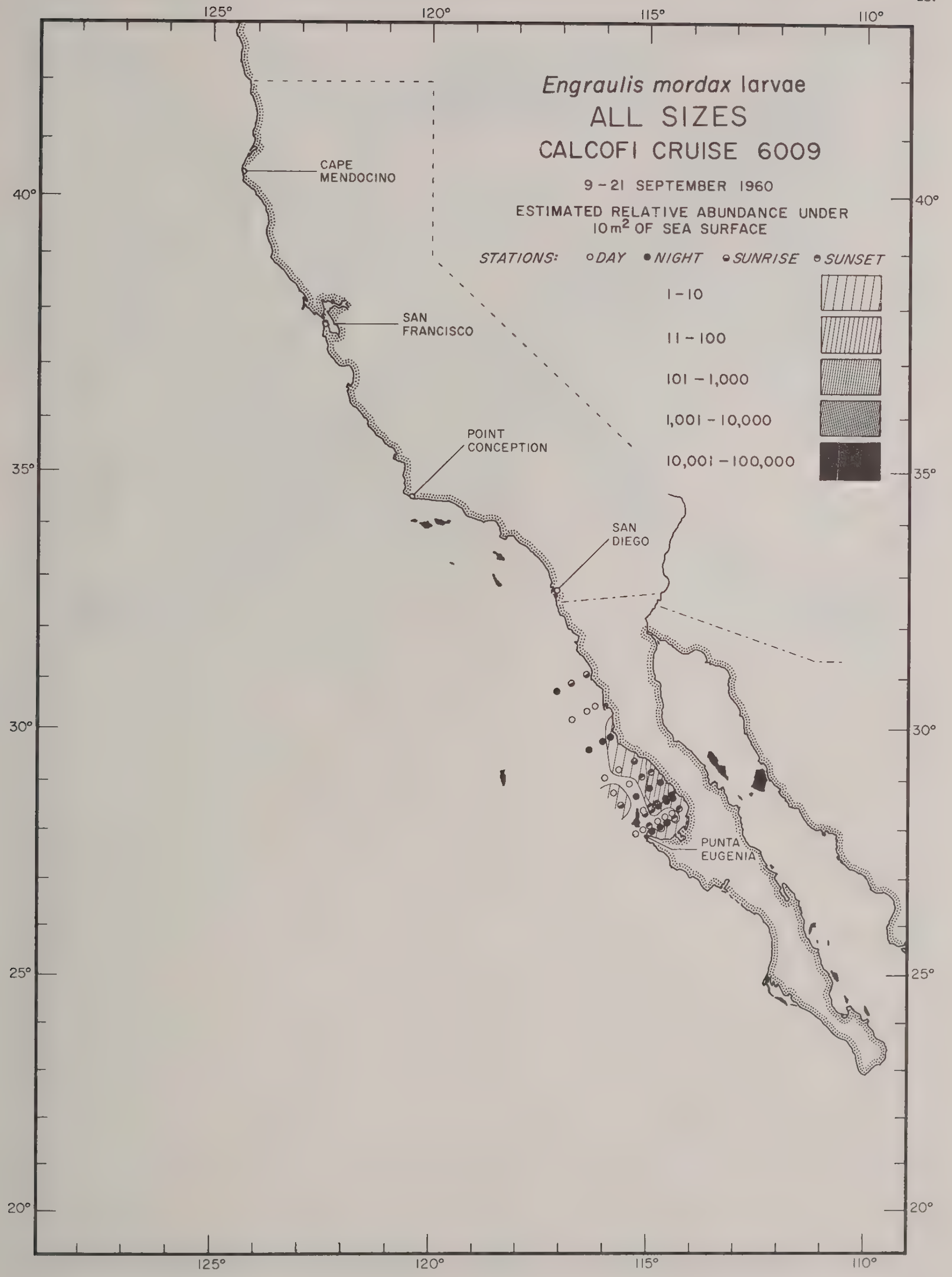
All Sizes
6008


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 6009
9 - 21 SEPTEMBER 1960
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◉ SUNRISE ◉ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

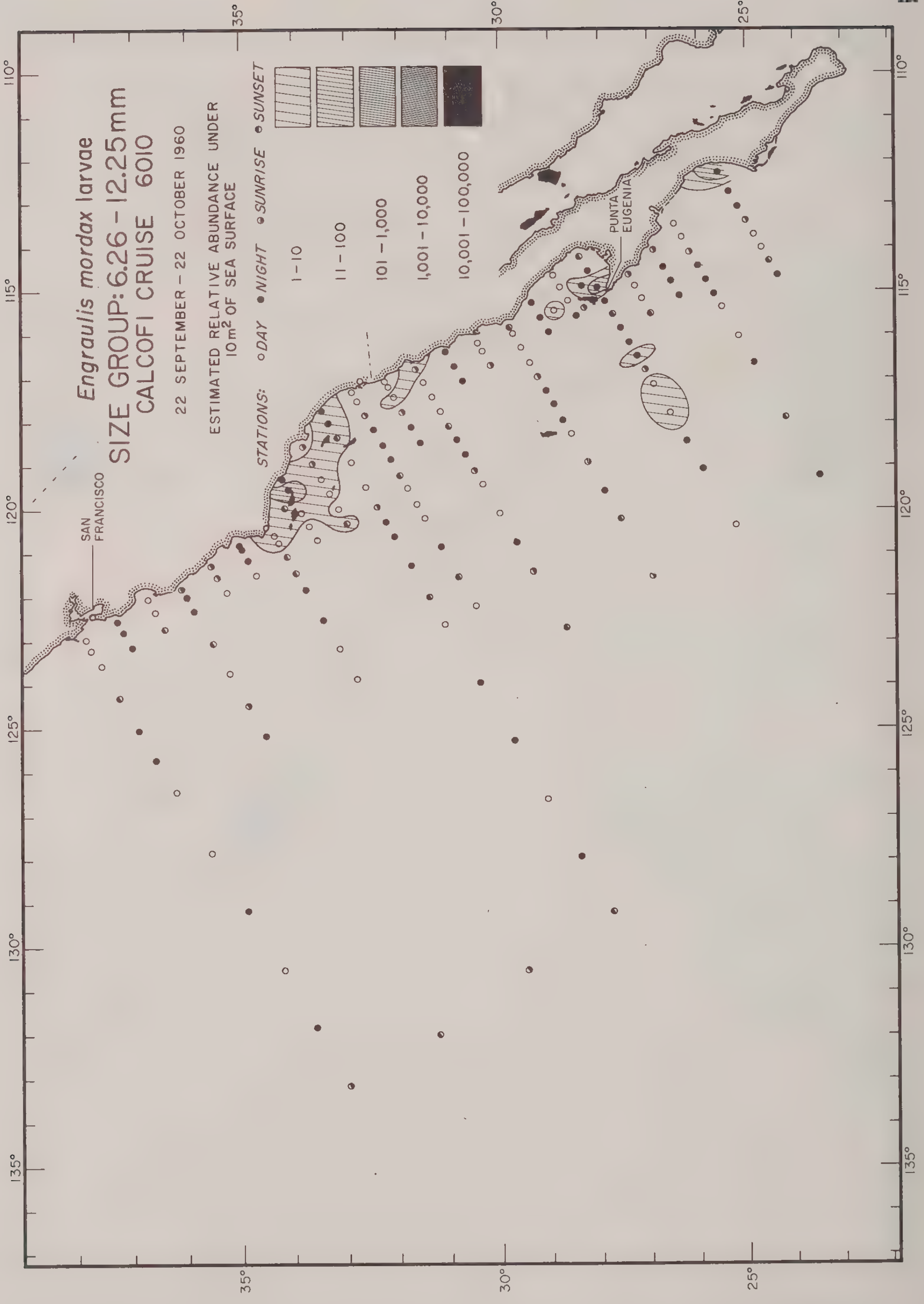
6009


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6009
9 – 21 SEPTEMBER 1960
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°

Engraulis mordax larvae

All Sizes

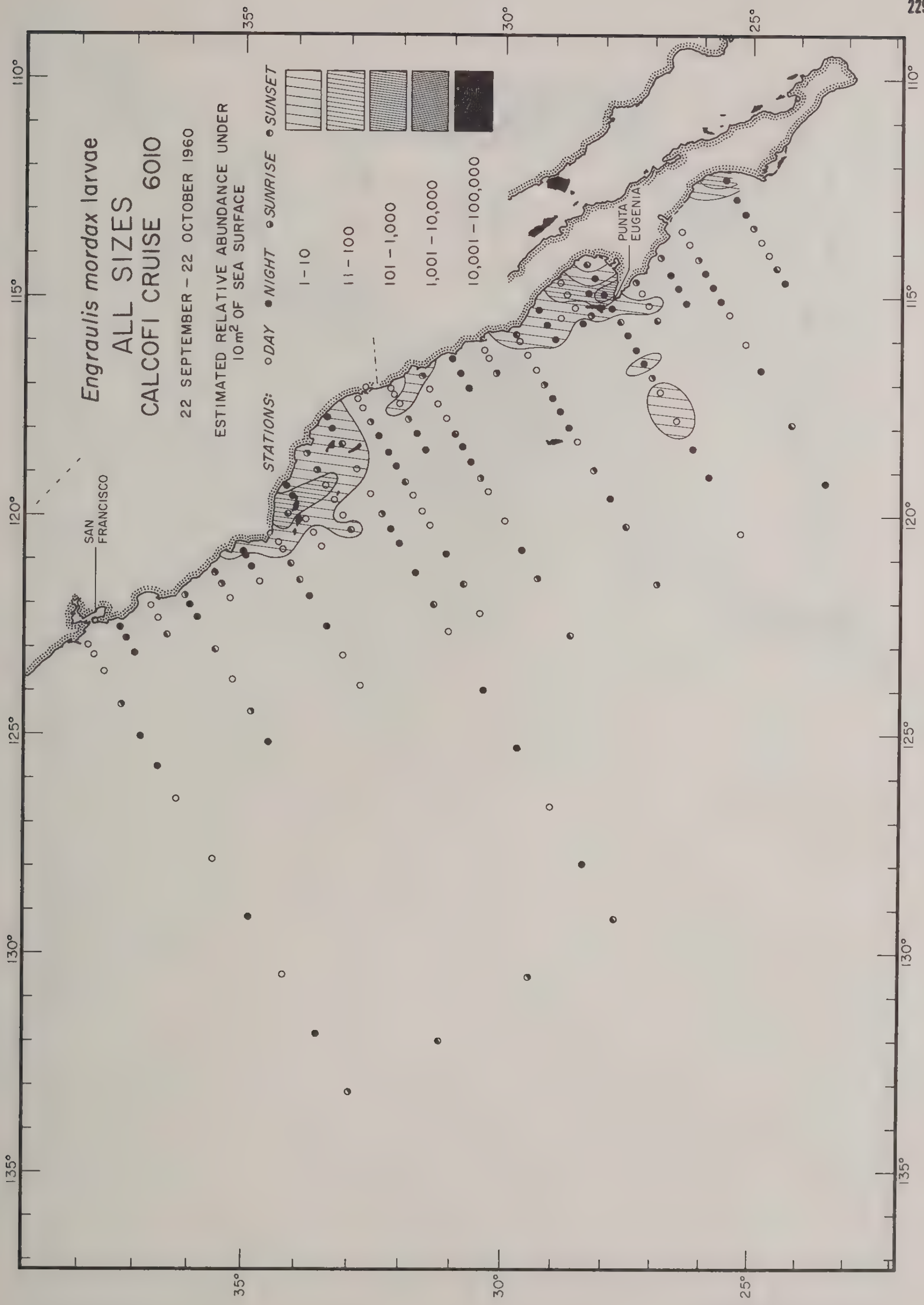
6009


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 6010
22 SEPTEMBER - 22 OCTOBER 1960
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
▨ 1-10
▨ 11-100
▨ 101-1,000
▨ 1,001-10,000
■ 10,001-100,000
SAN FRANCISCO
PUNTA EUGENIA
35°
30°
25°
110°
115°
120°
125°
130°
135°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

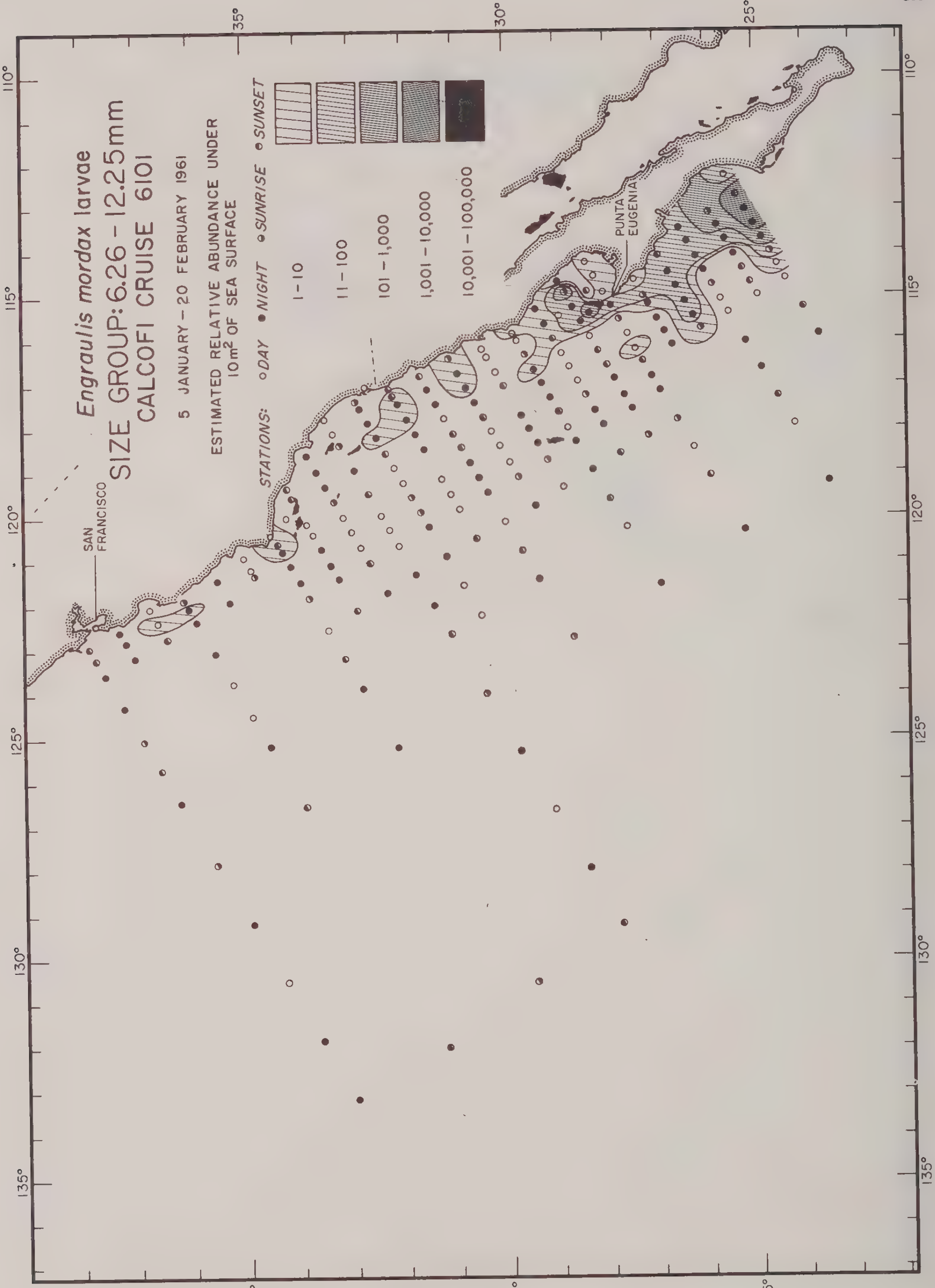
6010


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6010
22 SEPTEMBER – 22 OCTOBER 1960
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
SAN FRANCISCO
PUNTA EUGENIA
35°
30°
25°
110°
115°
120°
125°
130°
135°

Engraulis mordax larvae

All Sizes

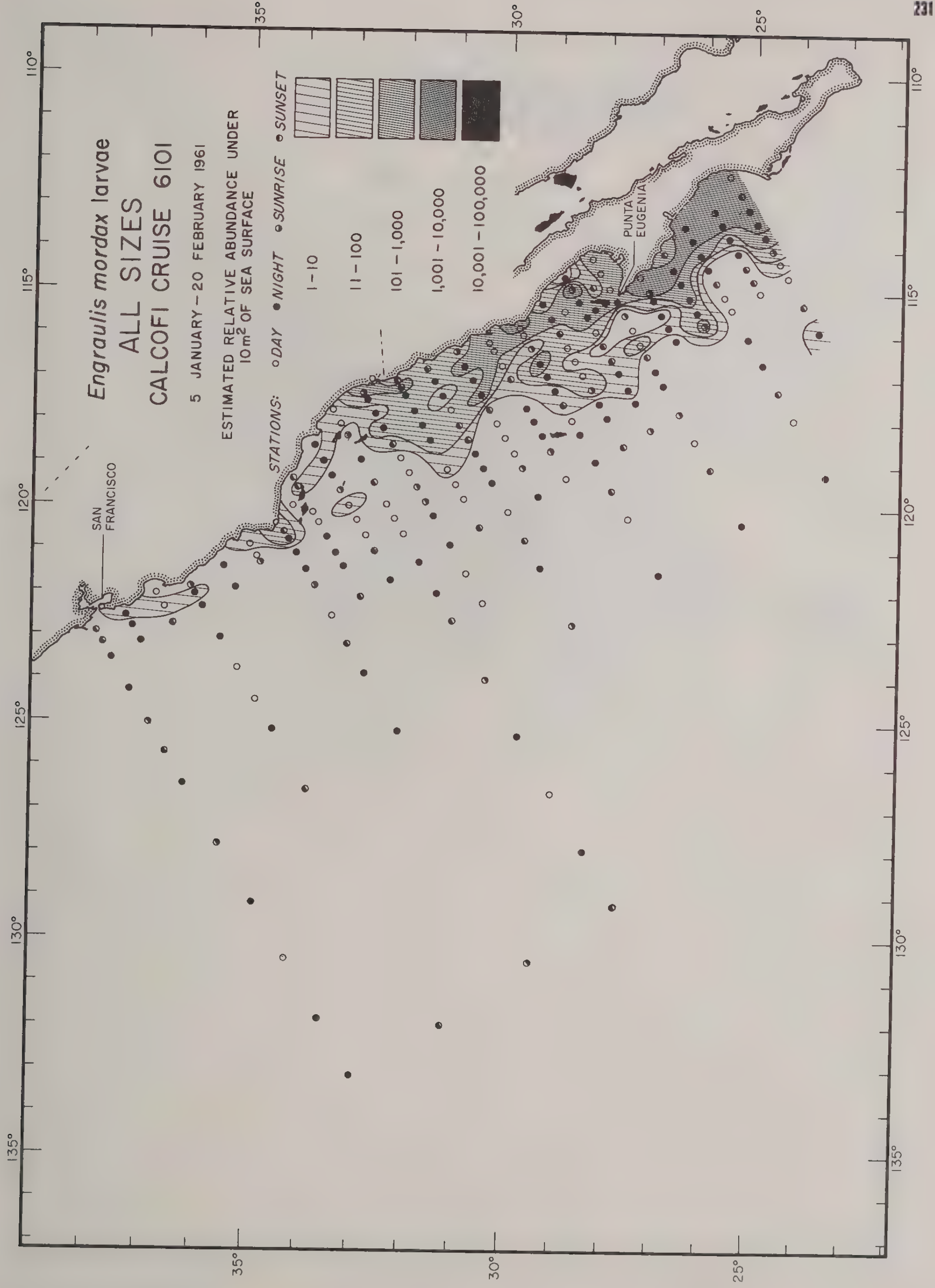
6010


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 6101
5 JANUARY - 20 FEBRUARY 1961
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
SAN FRANCISCO
PUNTA EUGENIA
35°
30°
25°
110°
115°
120°
125°
130°
135°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

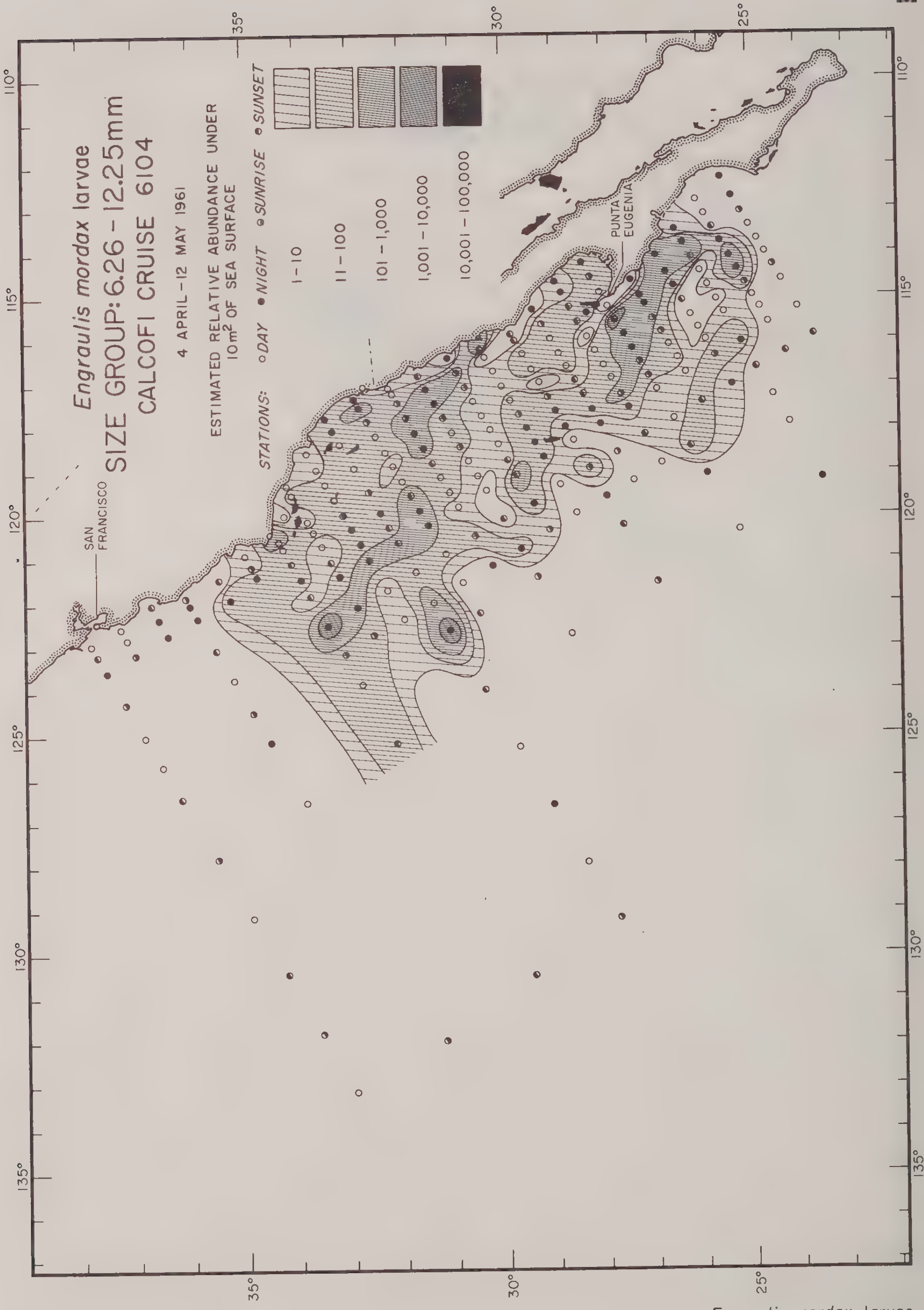
6101


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6101
5 JANUARY – 20 FEBRUARY 1961
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
SAN FRANCISCO
PUNTA EUGENIA
110°
115°
120°
125°
130°
135°
35°
30°
25°

Engraulis mordax larvae

All Sizes

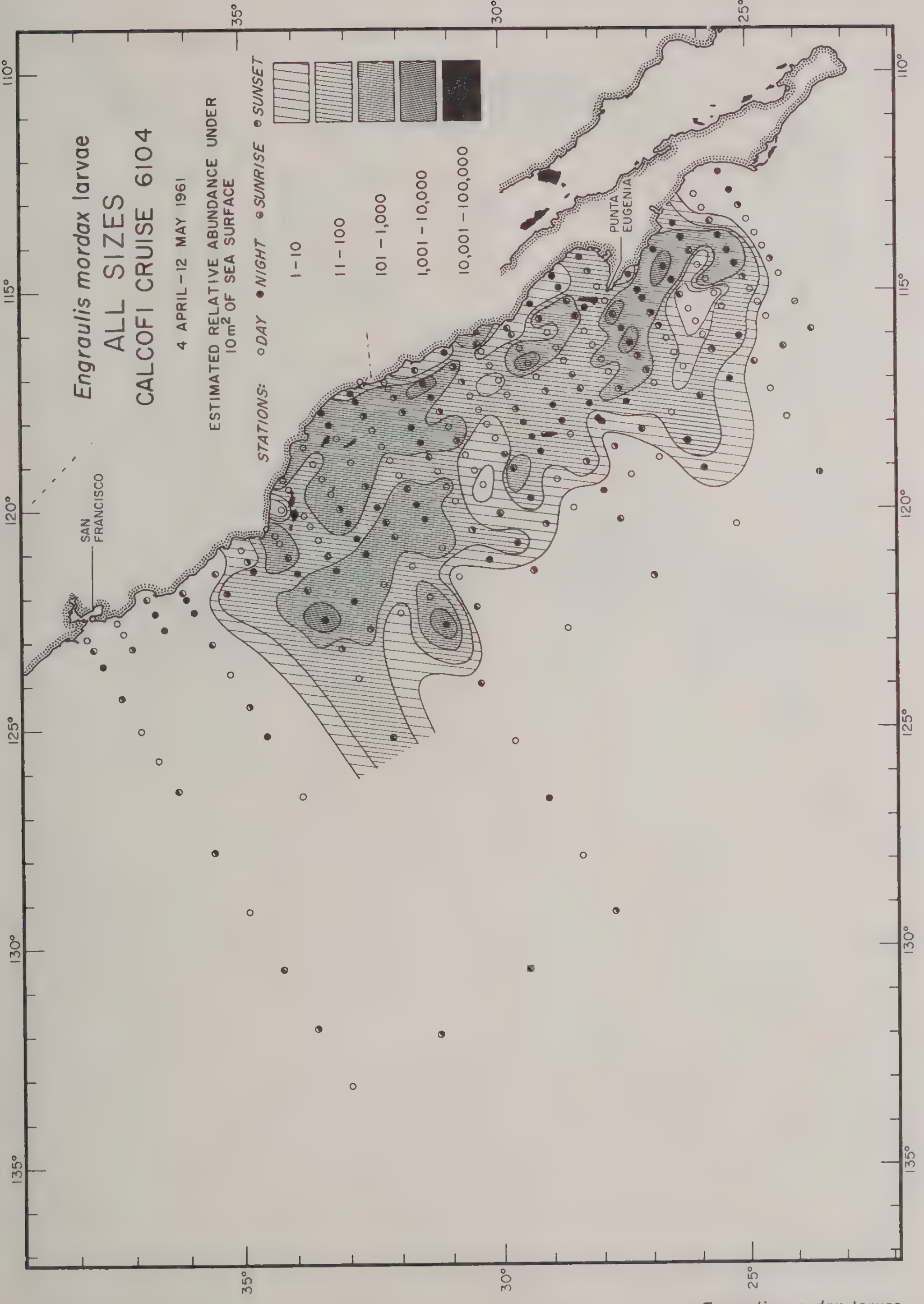
6101


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 6104
4 APRIL-12 MAY 1961
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◐SUNRISE ◑SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
SAN FRANCISCO
PUNTA EUGENIA
35°
30°
25°
110°
115°
120°
125°
130°
135°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

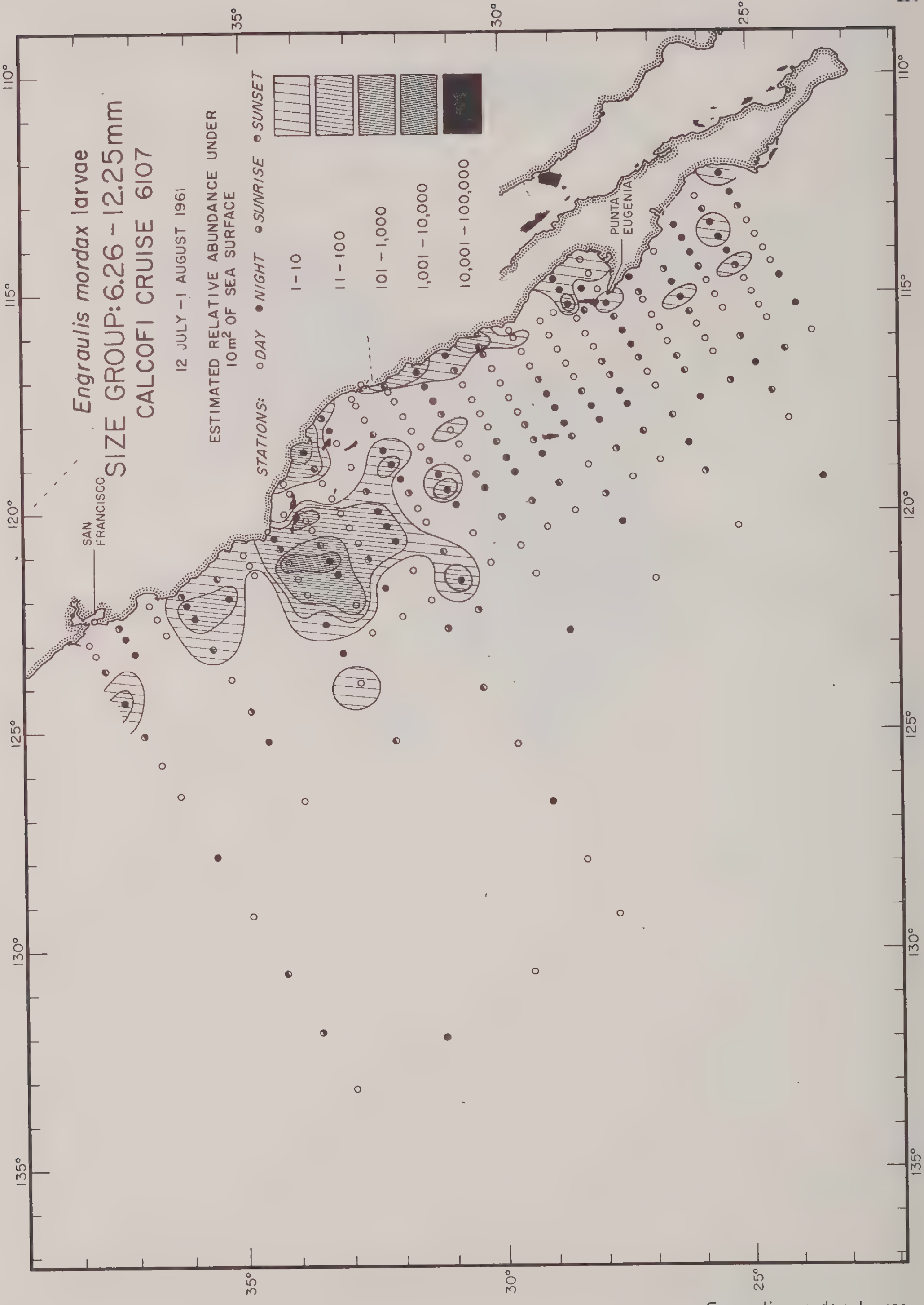
6104


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6104
4 APRIL - 12 MAY 1961
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m^2 OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
SAN FRANCISCO
PUNTA EUGENIA
35°
30°
25°
110°
115°
120°
125°
130°
135°

Engraulis mordax larvae

All Sizes

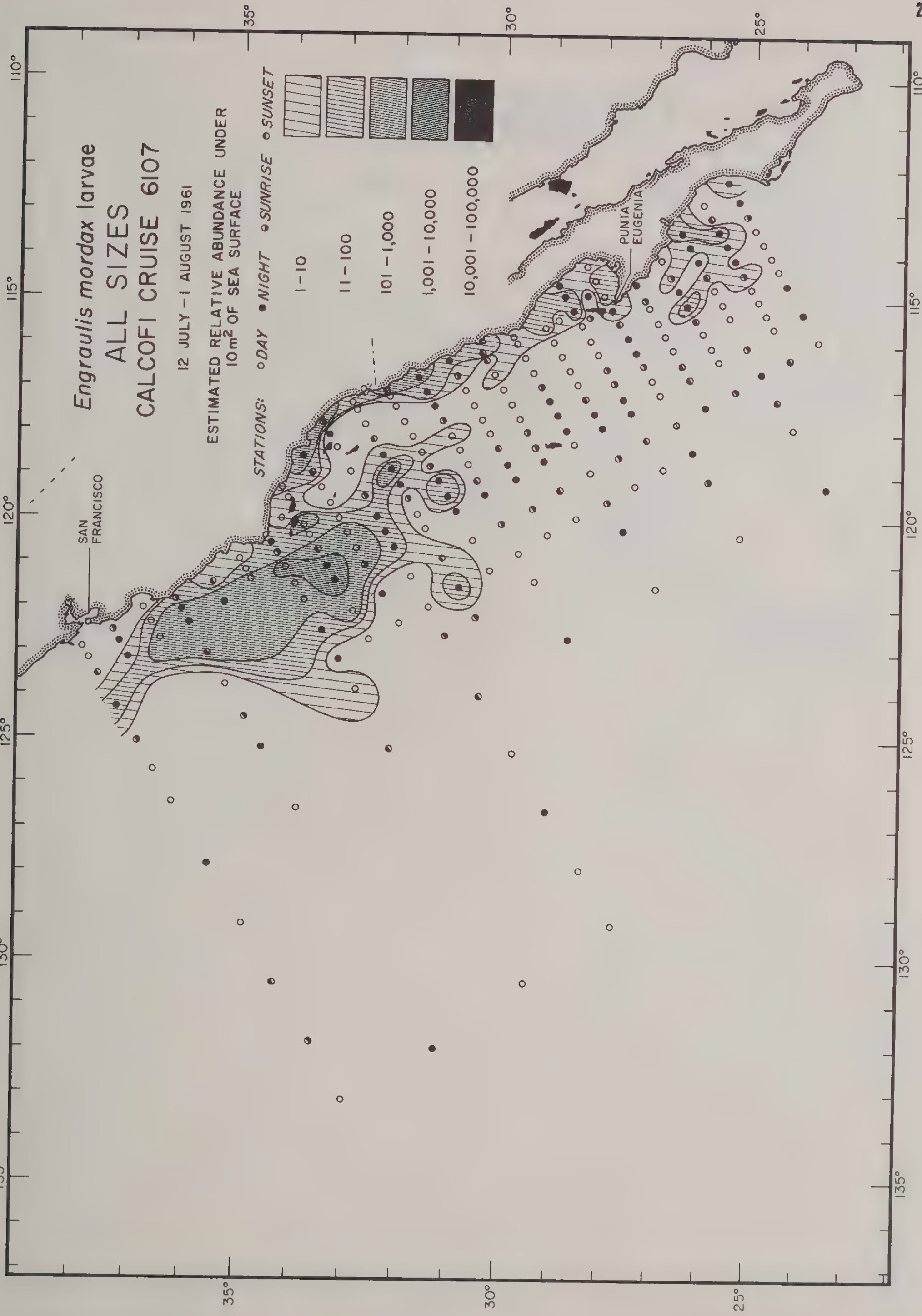
6104


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 6107
12 JULY - 1 AUGUST 1961
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◐ SUNSET
SAN FRANCISCO
PUNTA EUGENIA
35°
30°
25°
110°
115°
120°
125°
130°
135°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

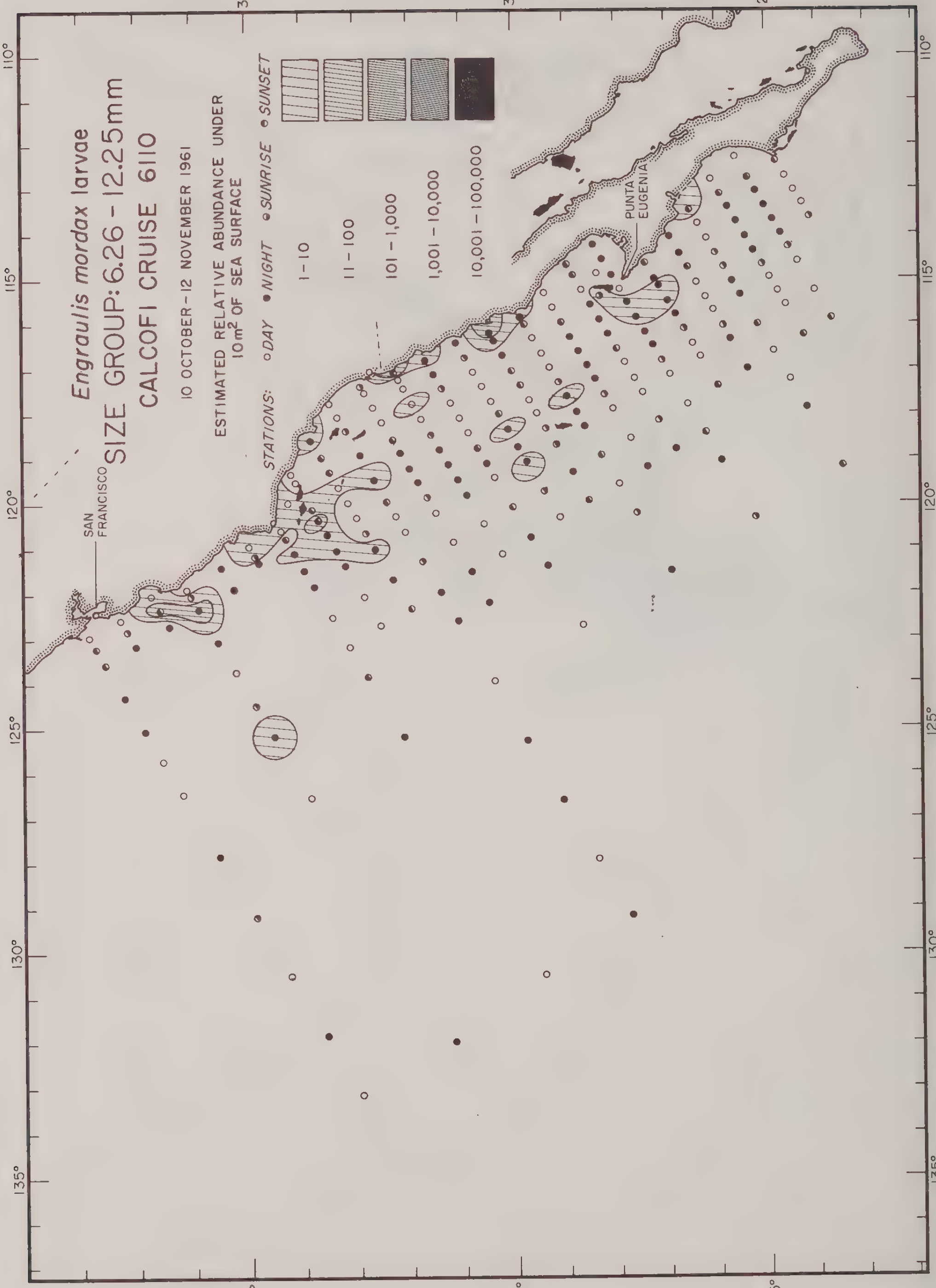
6107


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6107
12 JULY - 1 AUGUST 1961
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
SAN FRANCISCO
PUNTA EUGENIA
35°
30°
25°
110°
115°
120°
125°
130°
135°

Engraulis mordax larvae

All Sizes

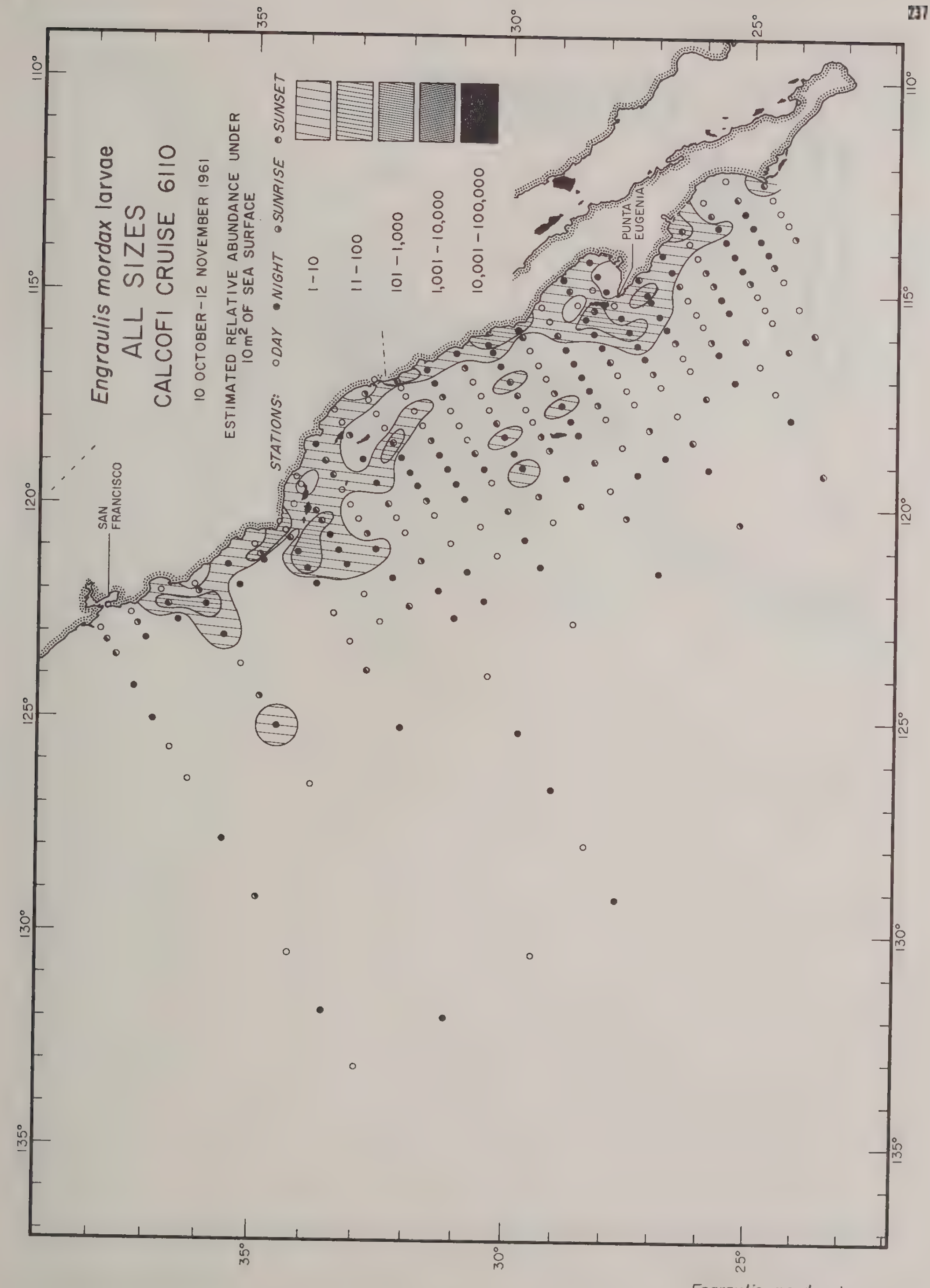
6107


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 6110
10 OCTOBER - 12 NOVEMBER 1961
ESTIMATED RELATIVE ABUNDANCE UNDER $10 m^2$ OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◐SUNRISE ◑SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
SAN FRANCISCO
PUNTA EUGENIA
35°
30°
25°
110°
115°
120°
125°
130°
135°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

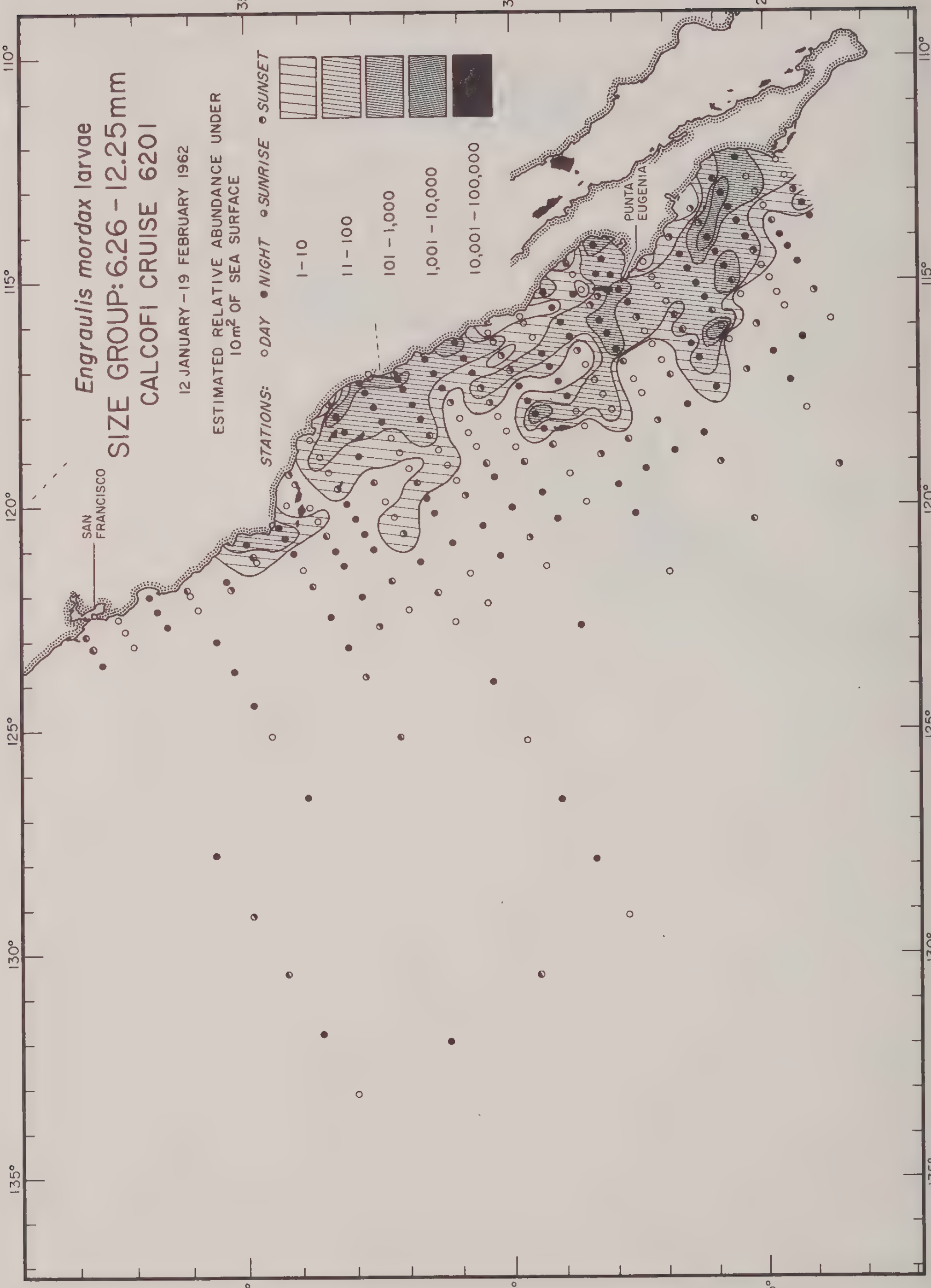
6110


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6110
10 OCTOBER-12 NOVEMBER 1961
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◐SUNRISE ◑SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
SAN FRANCISCO
PUNTA EUGENIA
35°
30°
25°
110°
115°
120°
125°
130°
135°

Engraulis mordax larvae

All Sizes

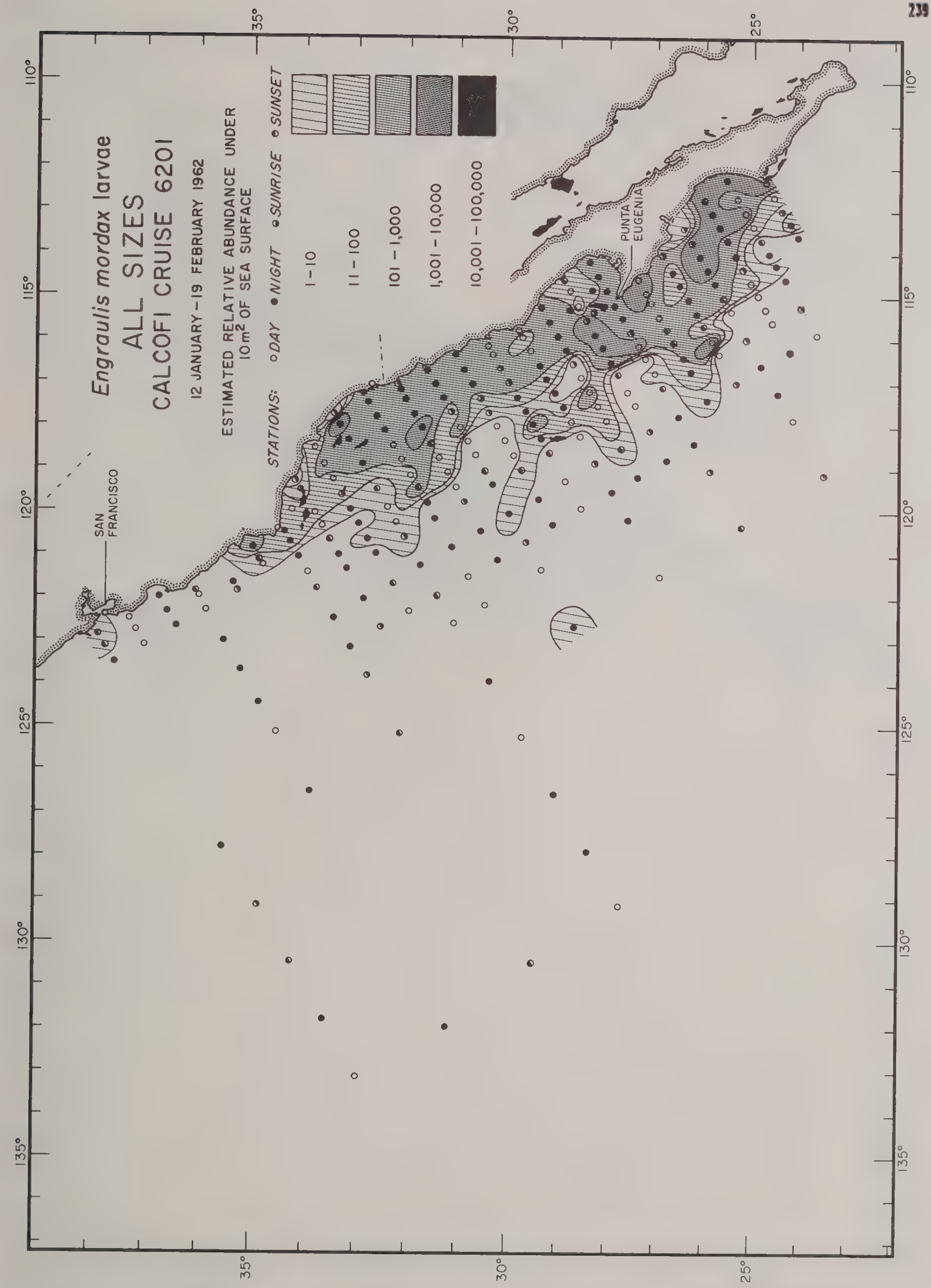
6110


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 6201
12 JANUARY - 19 FEBRUARY 1962
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
SAN FRANCISCO
PUNTA EUGENIA
35°
30°
25°
110°
115°
120°
125°
130°
135°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

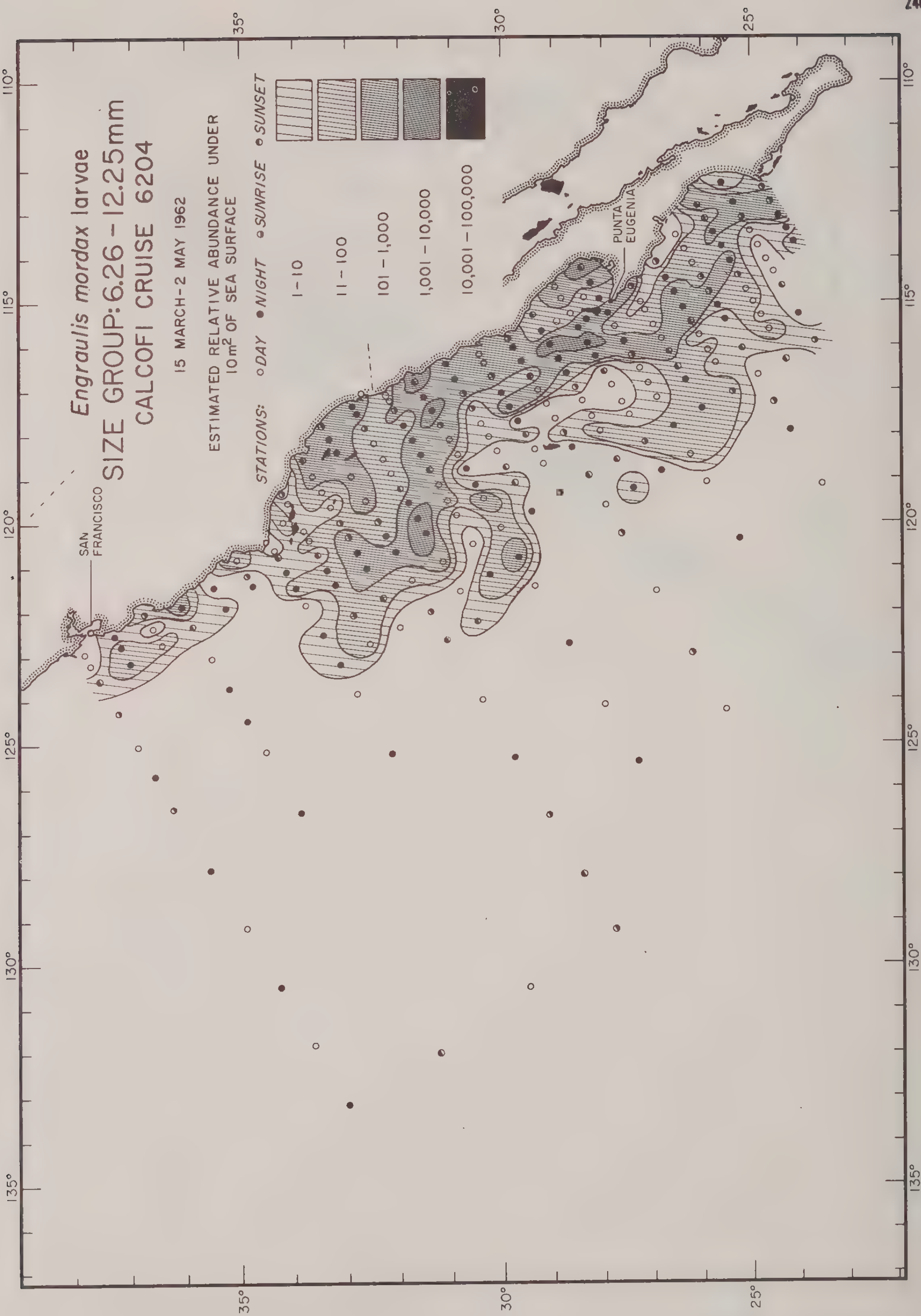
6201


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6201
12 JANUARY - 19 FEBRUARY 1962
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
SAN FRANCISCO
PUNTA EUGENIA
35°
30°
25°
110°
115°
120°
125°
130°
135°

Engraulis mordax larvae

All Sizes

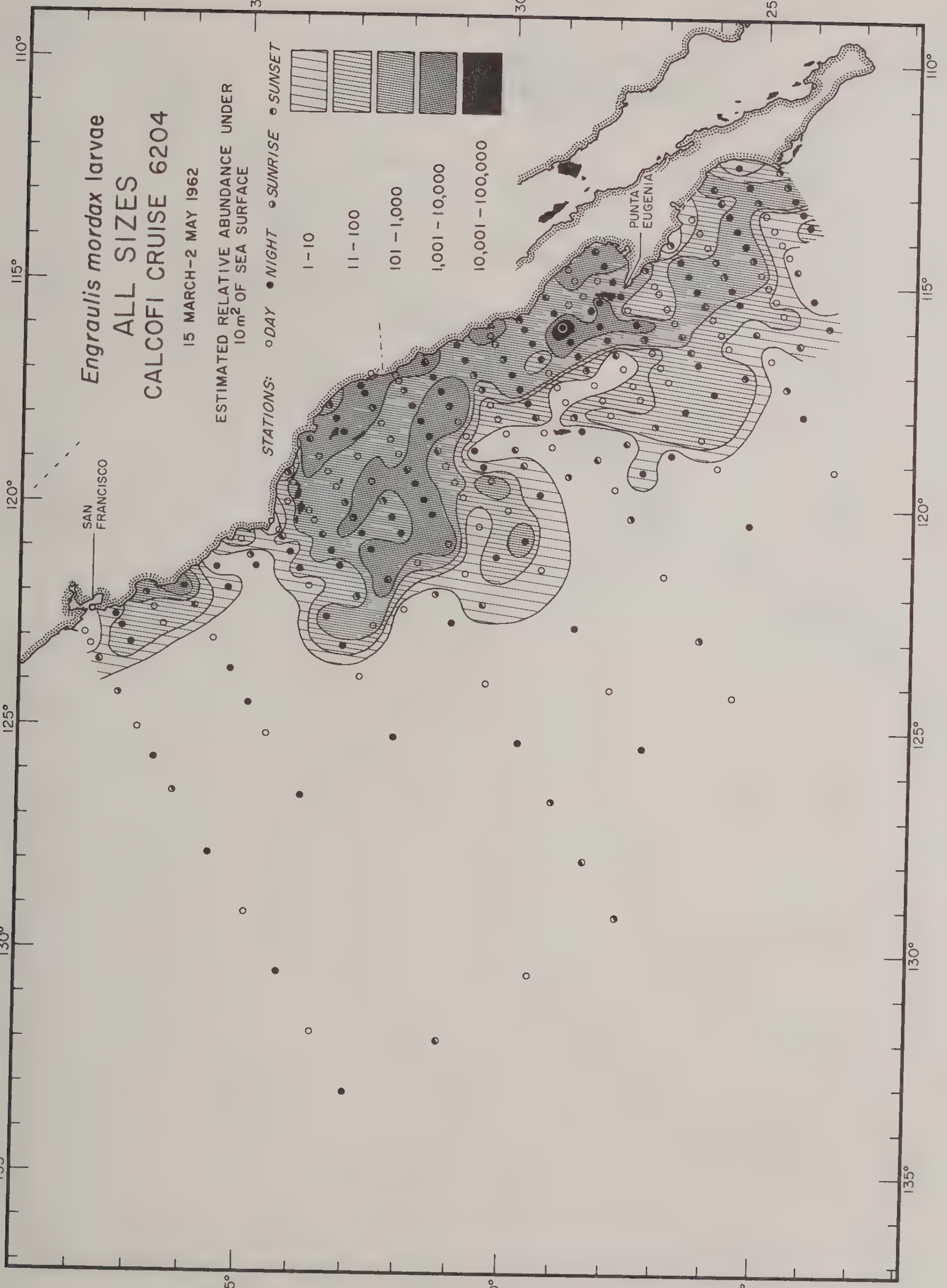
6201


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25 mm
CALCOFI CRUISE 6204
15 MARCH - 2 MAY 1962
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
SAN FRANCISCO
PUNTA EUGENIA
35°
30°
25°
110°
115°
120°
125°
130°
135°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

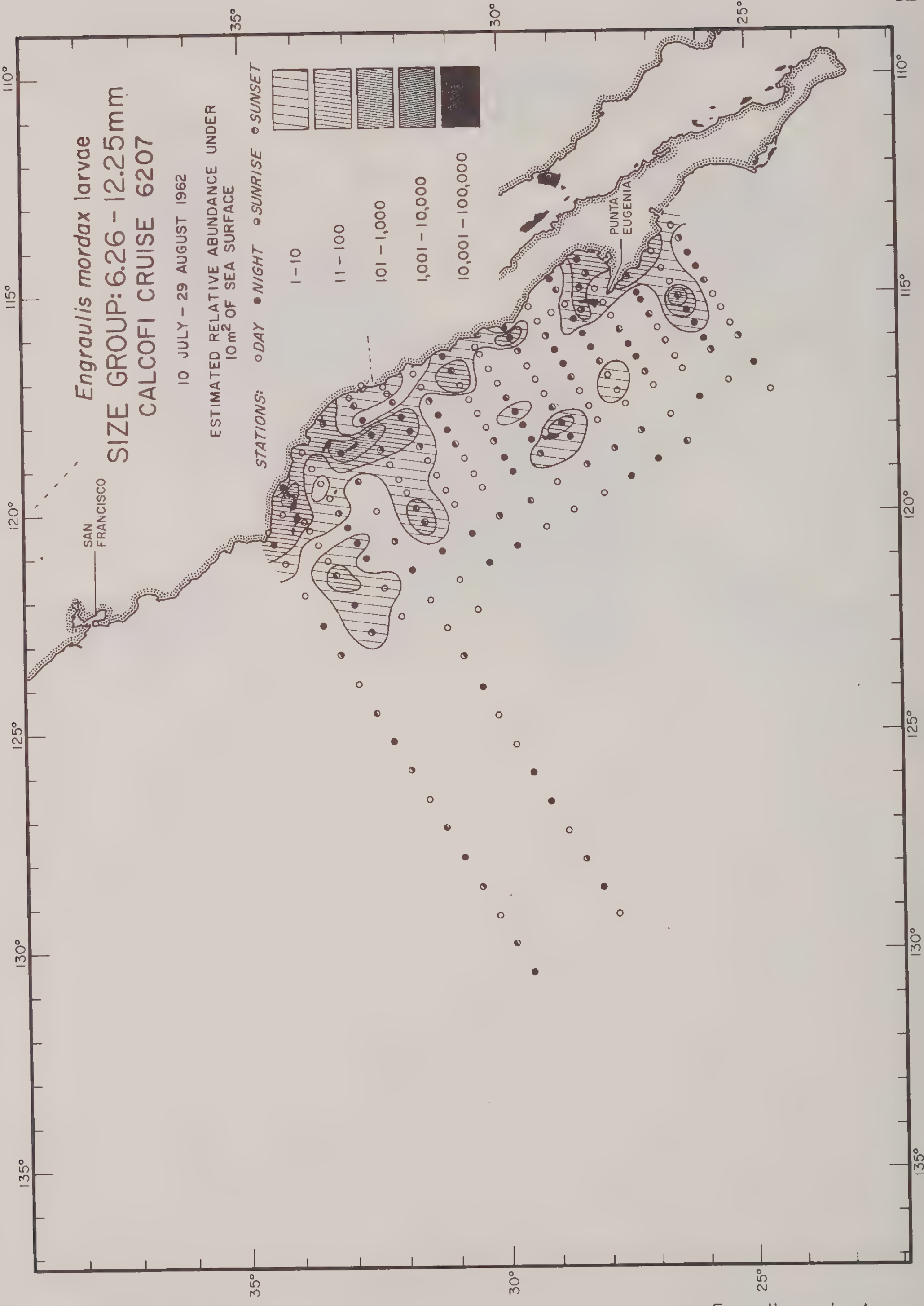
6204


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6204
15 MARCH–2 MAY 1962
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
STATIONS: ○DAY ●NIGHT ◐SUNRISE ◑SUNSET
SAN FRANCISCO
PUNTA EUGENIA
110°
115°
120°
125°
130°
135°
35°
30°
25°

Engraulis mordax larvae

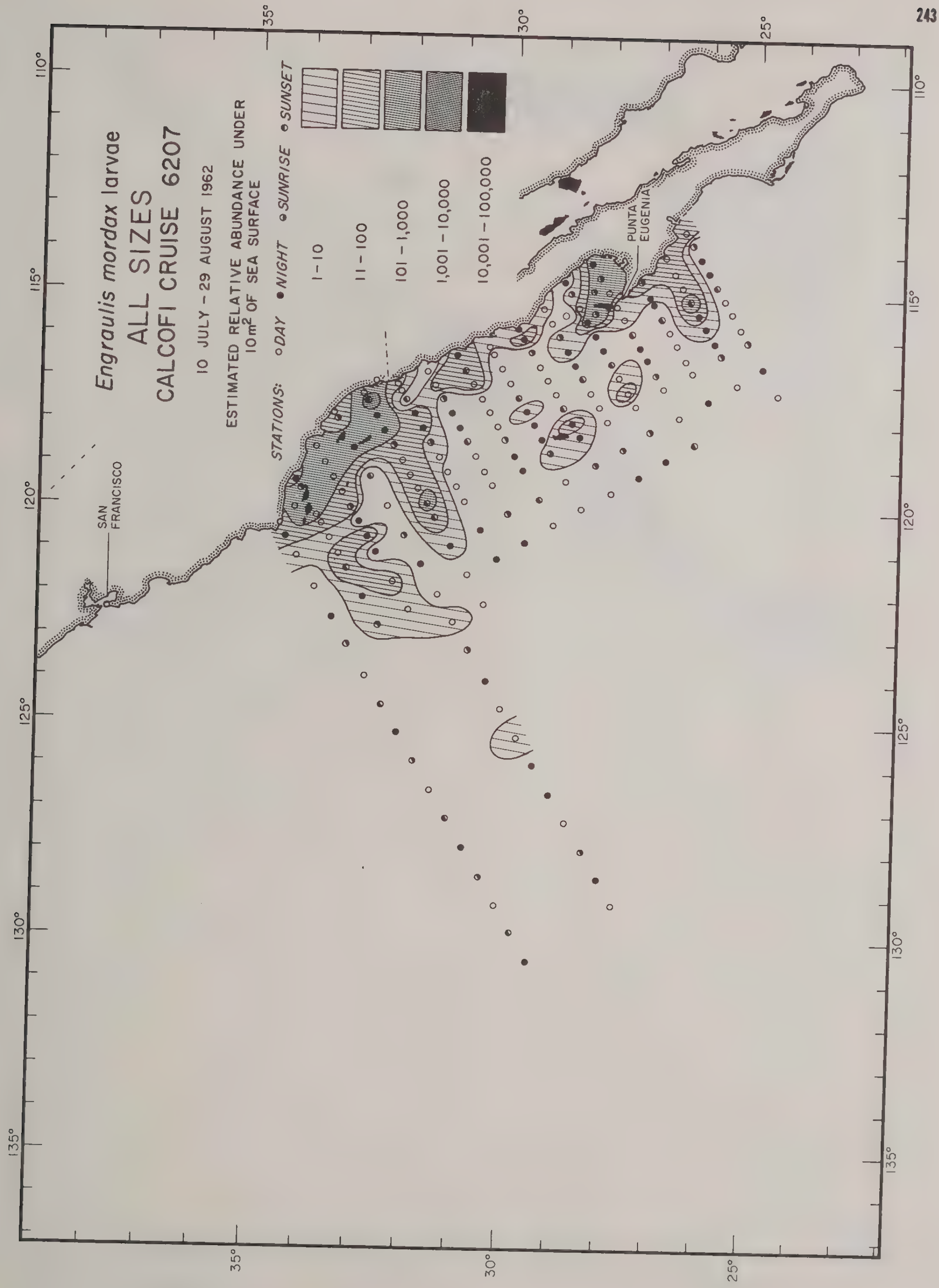
All Sizes

6204


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 6207
10 JULY - 29 AUGUST 1962
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◐SUNRISE ◑SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
SAN FRANCISCO
PUNTA EUGENIA
35°
30°
25°
110°
115°
120°
125°
130°
135°

Engraulis mordax larvae

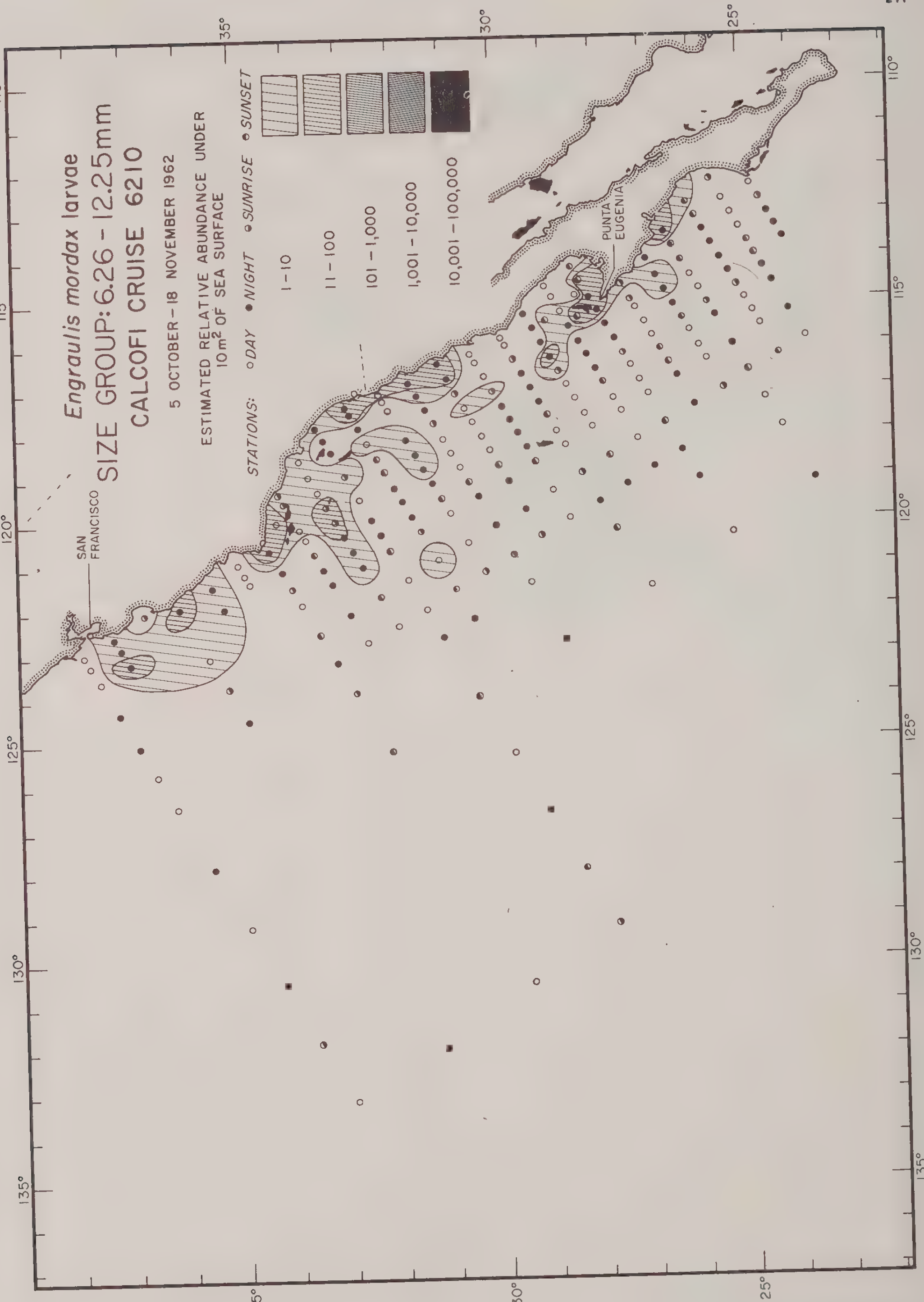
Size Group: 6.26-12.25mm
6207


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6207
10 JULY - 29 AUGUST 1962
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
SAN FRANCISCO
PUNTA EUGENIA
35°
30°
25°
110°
115°
120°
125°
130°
135°

Engraulis mordax larvae

All Sizes

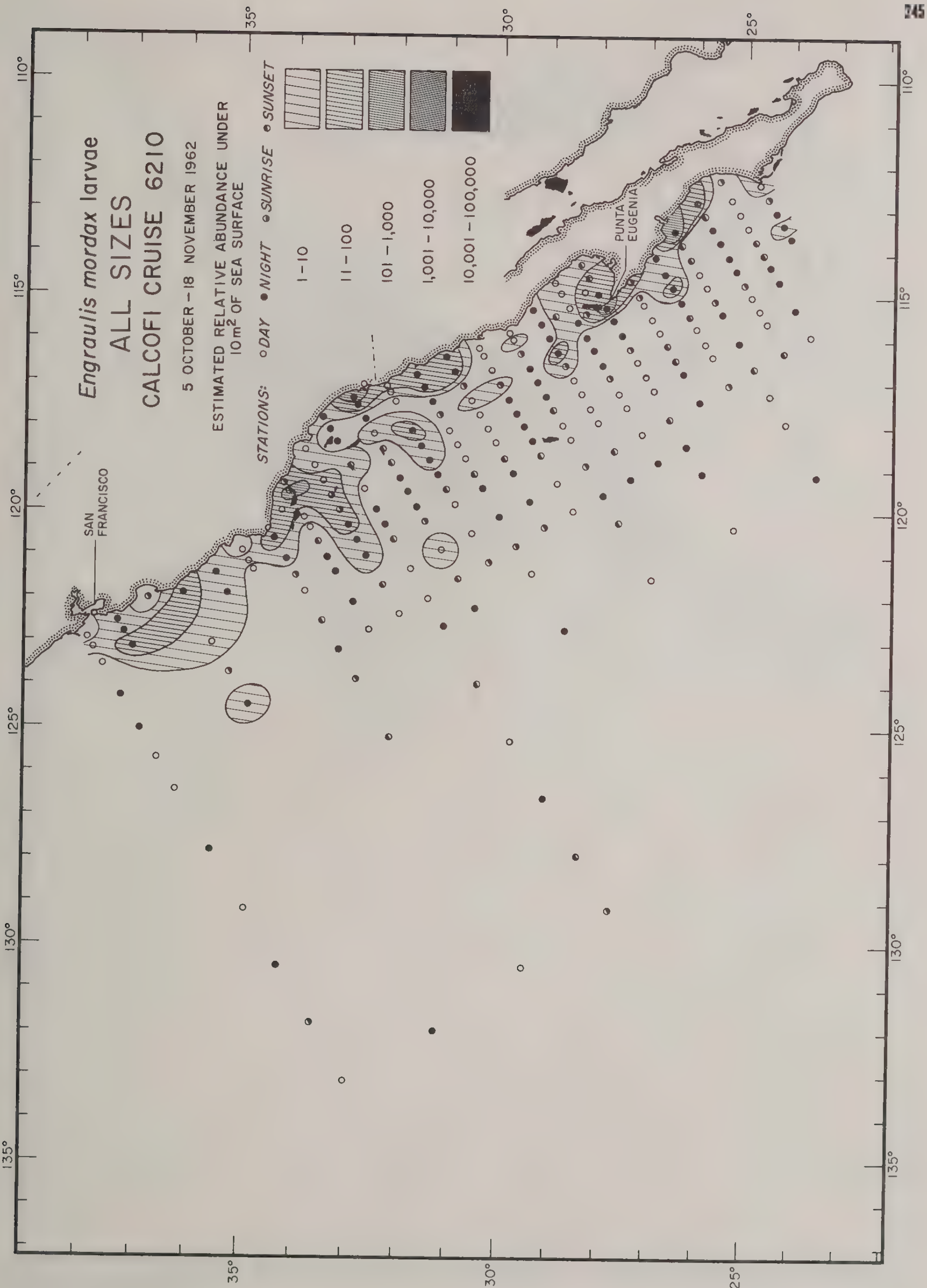
6207


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 6210
5 OCTOBER - 18 NOVEMBER 1962
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 - 10
11 - 100
101 - 1,000
1,001 - 10,000
10,001 - 100,000
SAN FRANCISCO
PUNTA EUGENIA
35°
30°
25°
110°
115°
120°
125°
130°
135°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

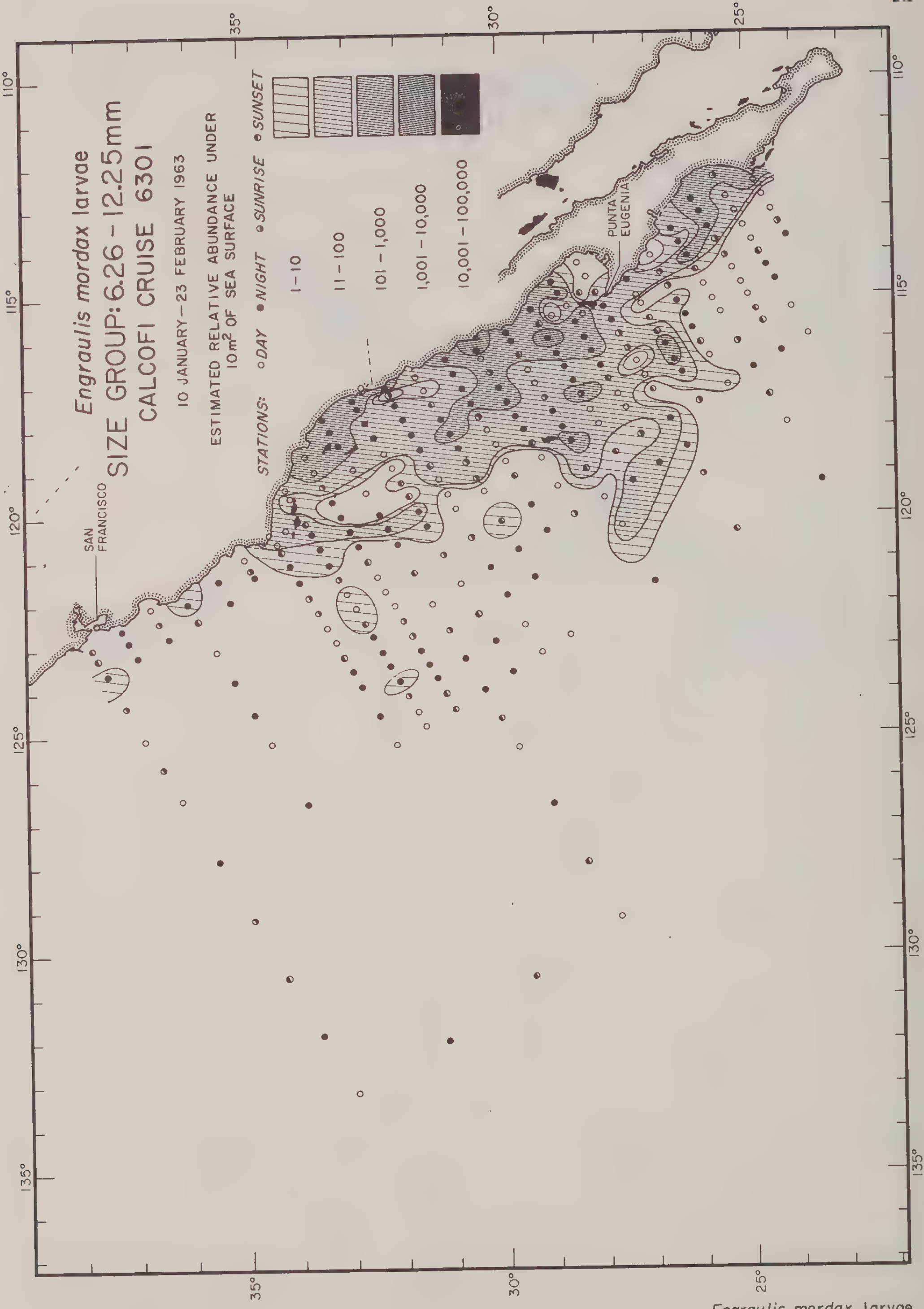
6210


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6210
5 OCTOBER – 18 NOVEMBER 1962
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 – 10
11 – 100
101 – 1,000
1,001 – 10,000
10,001 – 100,000
SAN FRANCISCO
PUNTA EUGENIA
35°
30°
25°
110°
115°
120°
125°
130°
135°

Engraulis mordax larvae

All Sizes

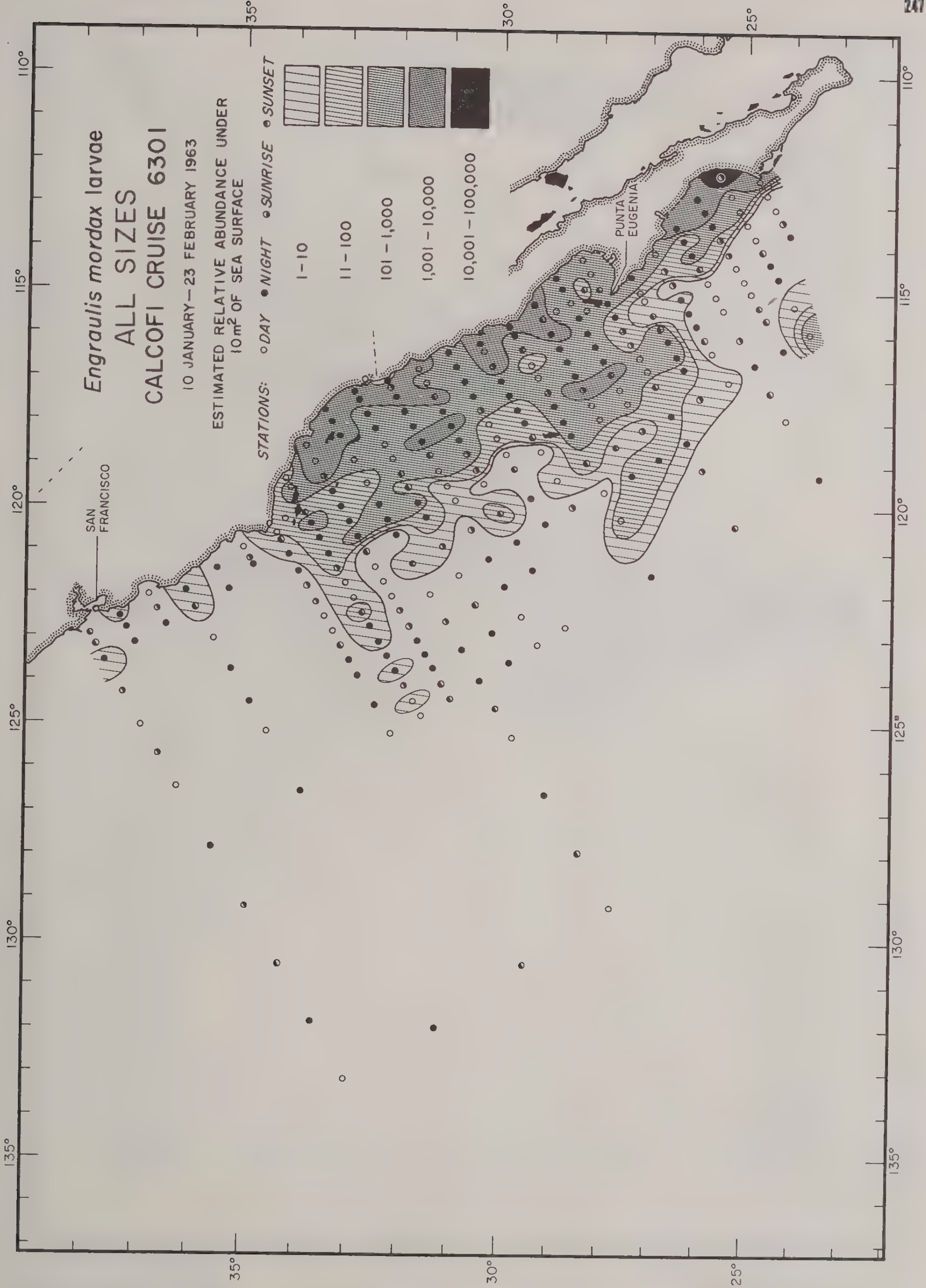
6210


Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 6301
10 JANUARY—23 FEBRUARY 1963
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
SAN FRANCISCO
PUNTA EUGENIA
35°
30°
25°
110°
115°
120°
125°
130°
135°

Engraulis mordax larvae

Size Group: 6.26-12.25mm

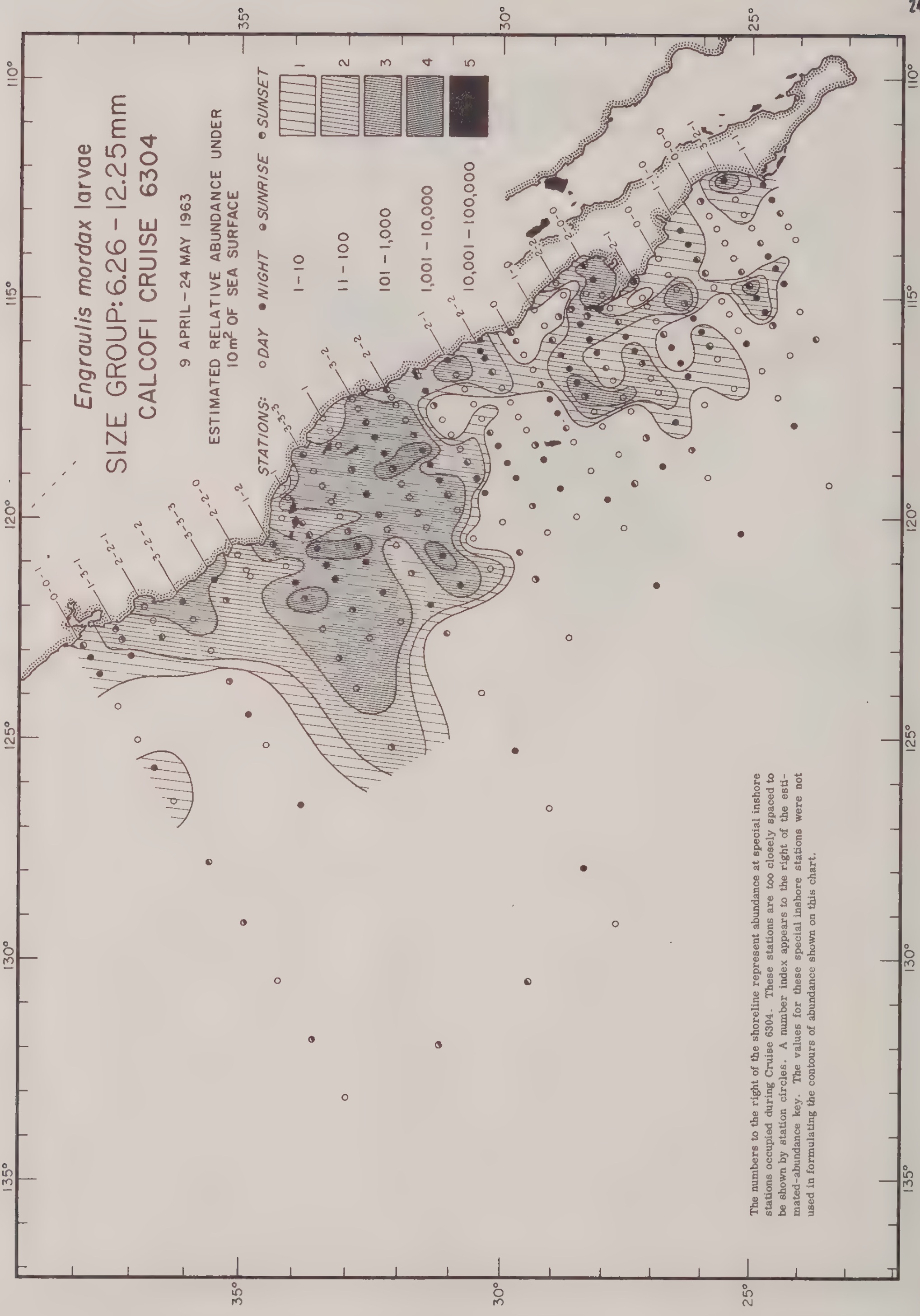
6301


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6301
10 JANUARY—23 FEBRUARY 1963
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
SAN FRANCISCO
PUNTA EUGENIA
35°
30°
25°
110°
115°
120°
125°
130°
135°

Engraulis mordax larvae

All Sizes

6301

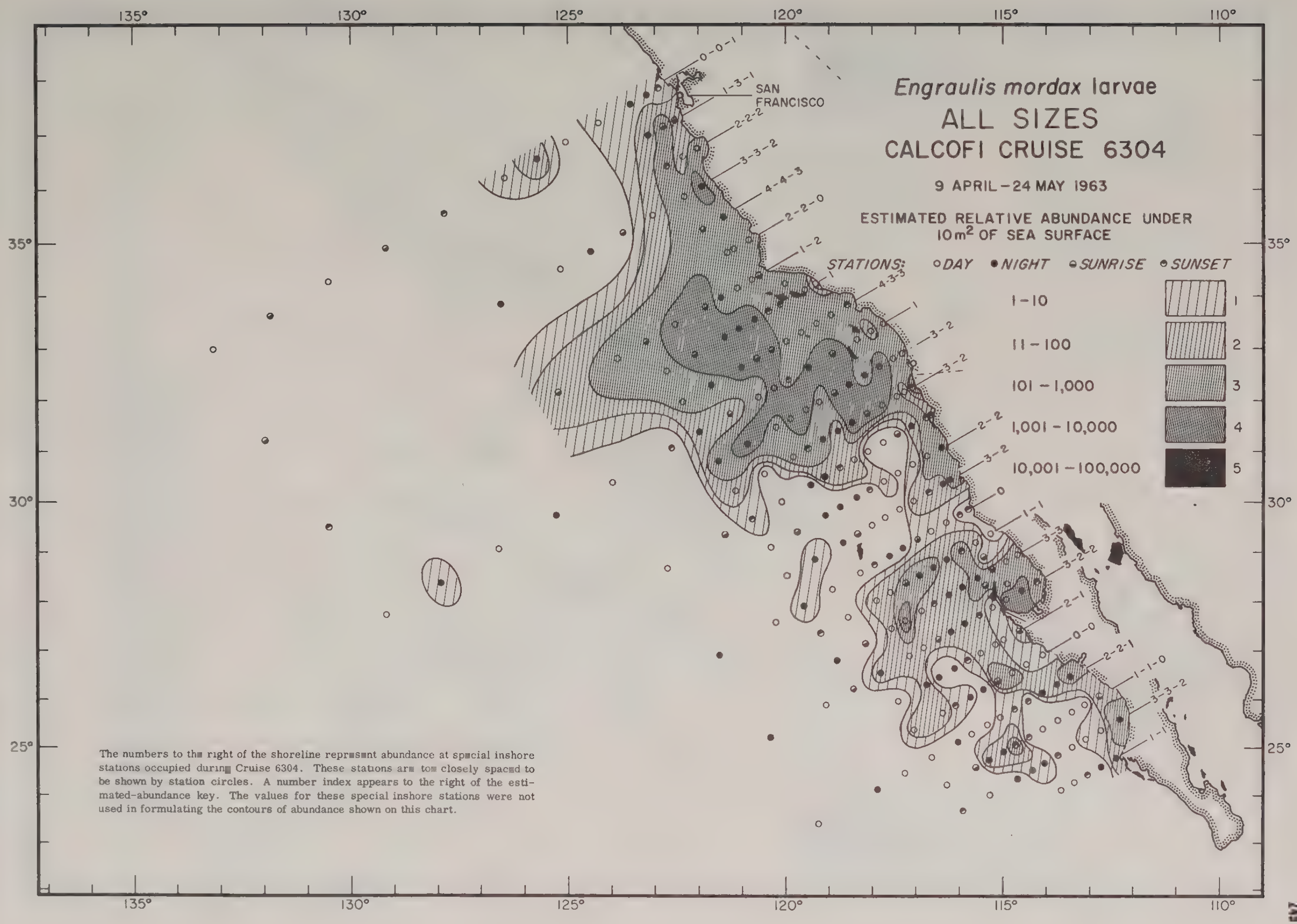

Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 6304
9 APRIL – 24 MAY 1963
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 1 - 10
2 11 - 100
3 101 - 1,000
4 1,001 - 10,000
5 10,001 - 100,000
110°
115°
120°
125°
130°
135°
35°
30°
25°

The numbers to the right of the shoreline represent abundance at special inshore stations occupied during Cruise 6304. These stations are too closely spaced to be shown by station circles. A number index appears to the right of the estimated-abundance key. The values for these special inshore stations were not used in formulating the contours of abundance shown on this chart.

Engraulis mordax larvae

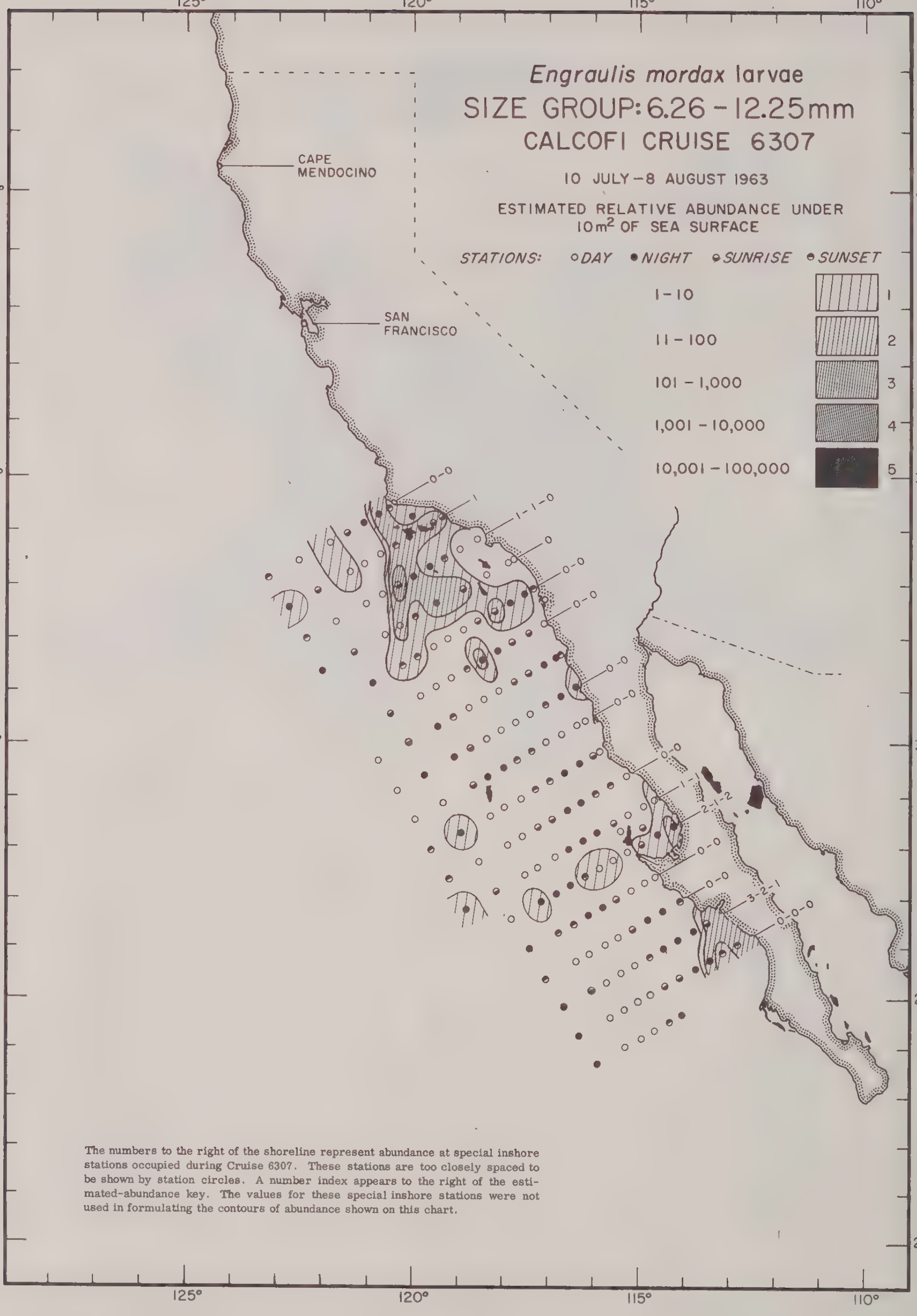
Size Group: 6.26-12.25mm

6304


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6304
9 APRIL – 24 MAY 1963
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1-10 1
11-100 2
101-1,000 3
1,001-10,000 4
10,001-100,000 5
SAN FRANCISCO
0-0-1
1-3-1
2-2-2
3-3-2
4-4-3
2-2-0
1-2
1
4-3-3
1
3-2
3-2
2-2
3-2
0
1-1
3-3
3-2-2
2-1
0-0
2-2-1
1-1-0
3-3-2
1-1
135°
130°
125°
120°
115°
110°
35°
30°
25°

The numbers to the right of the shoreline represent abundance at special inshore stations occupied during Cruise 6304. These stations are too closely spaced to be shown by station circles. A number index appears to the right of the estimated-abundance key. The values for these special inshore stations were not used in formulating the contours of abundance shown on this chart.

Engraulis mordax larvae
All Sizes
6304

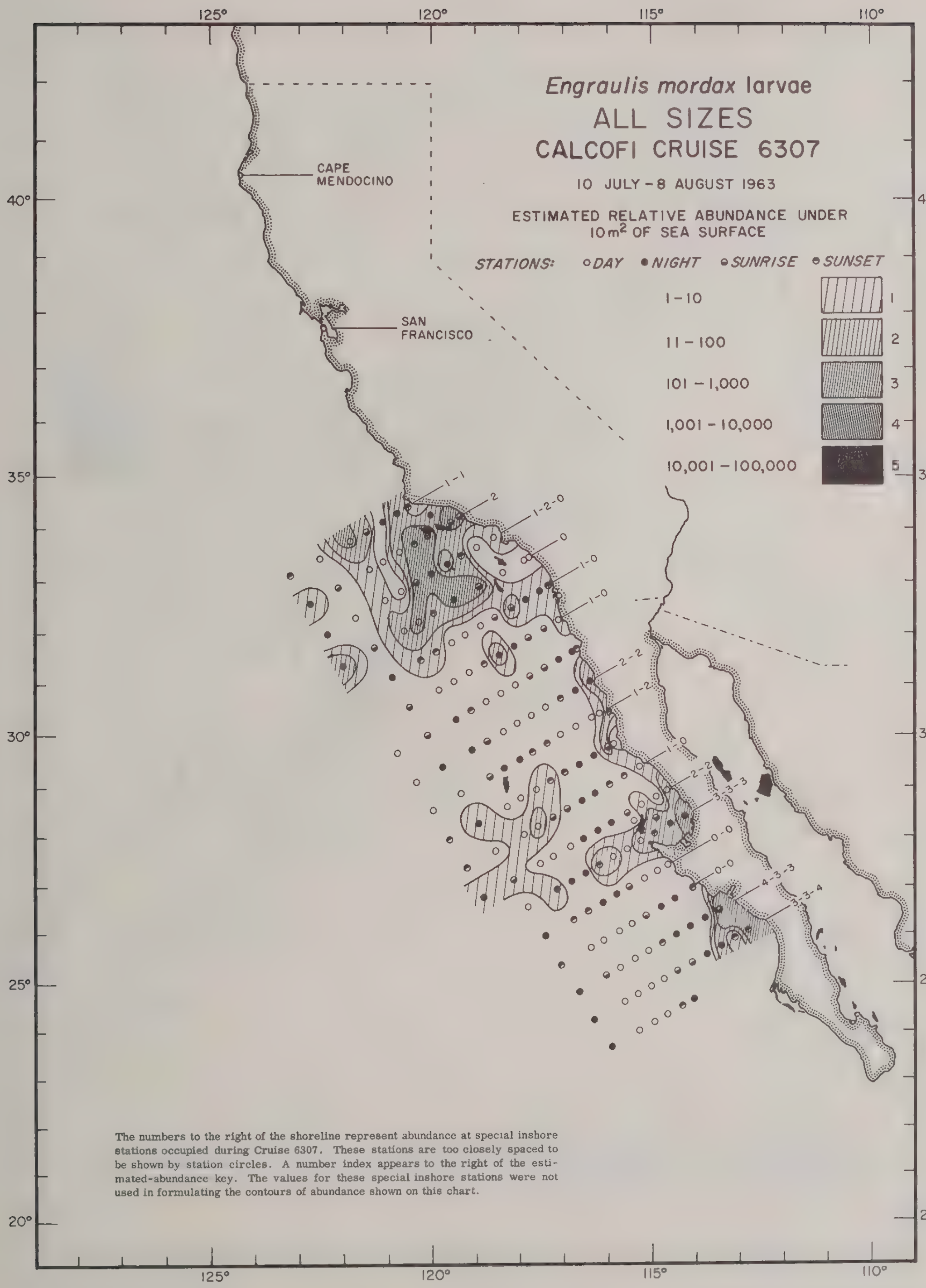

Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 6307
10 JULY – 8 AUGUST 1963
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1 - 10 ▨ 1
11 - 100 ▨ 2
101 - 1,000 ▨ 3
1,001 - 10,000 ▨ 4
10,001 - 100,000 ■ 5
CAPE MENDOCINO
SAN FRANCISCO
125°
120°
115°
110°
40°
35°
30°
25°
20°
0-0
1
1-1-0
0
0-0
0-0
0-0
0-0
0-0
1-1
2-1-2
0-0
0-0
3-2-1
0-0-0

The numbers to the right of the shoreline represent abundance at special inshore stations occupied during Cruise 6307. These stations are too closely spaced to be shown by station circles. A number index appears to the right of the estimated-abundance key. The values for these special inshore stations were not used in formulating the contours of abundance shown on this chart.

Engraulis mordax larvae

Size Group: 6.26-12.25mm

6307

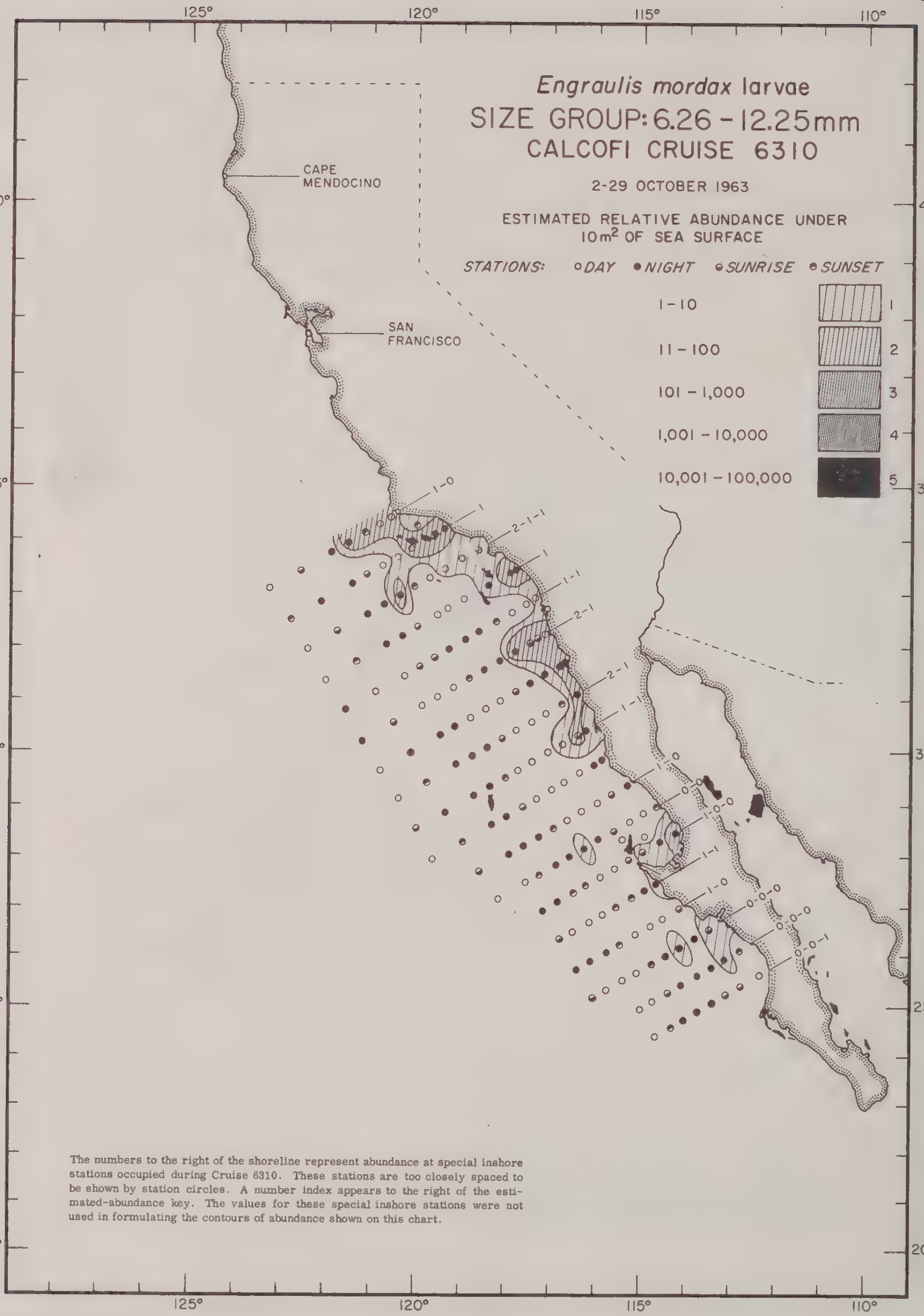

Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6307
10 JULY – 8 AUGUST 1963
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 – 10 1
11 – 100 2
101 – 1,000 3
1,001 – 10,000 4
10,001 – 100,000 5
CAPE MENDOCINO
SAN FRANCISCO
125°
120°
115°
110°
40°
35°
30°
25°
20°
1-1
2
1-2-0
0
1-0
1-0
2-2
1-2
1-0
2-2
3-3-3
0-0
0-0
4-3-3
3-3-4

The numbers to the right of the shoreline represent abundance at special inshore stations occupied during Cruise 6307. These stations are too closely spaced to be shown by station circles. A number index appears to the right of the estimated-abundance key. The values for these special inshore stations were not used in formulating the contours of abundance shown on this chart.

Engraulis mordax larvae

All Sizes

6307

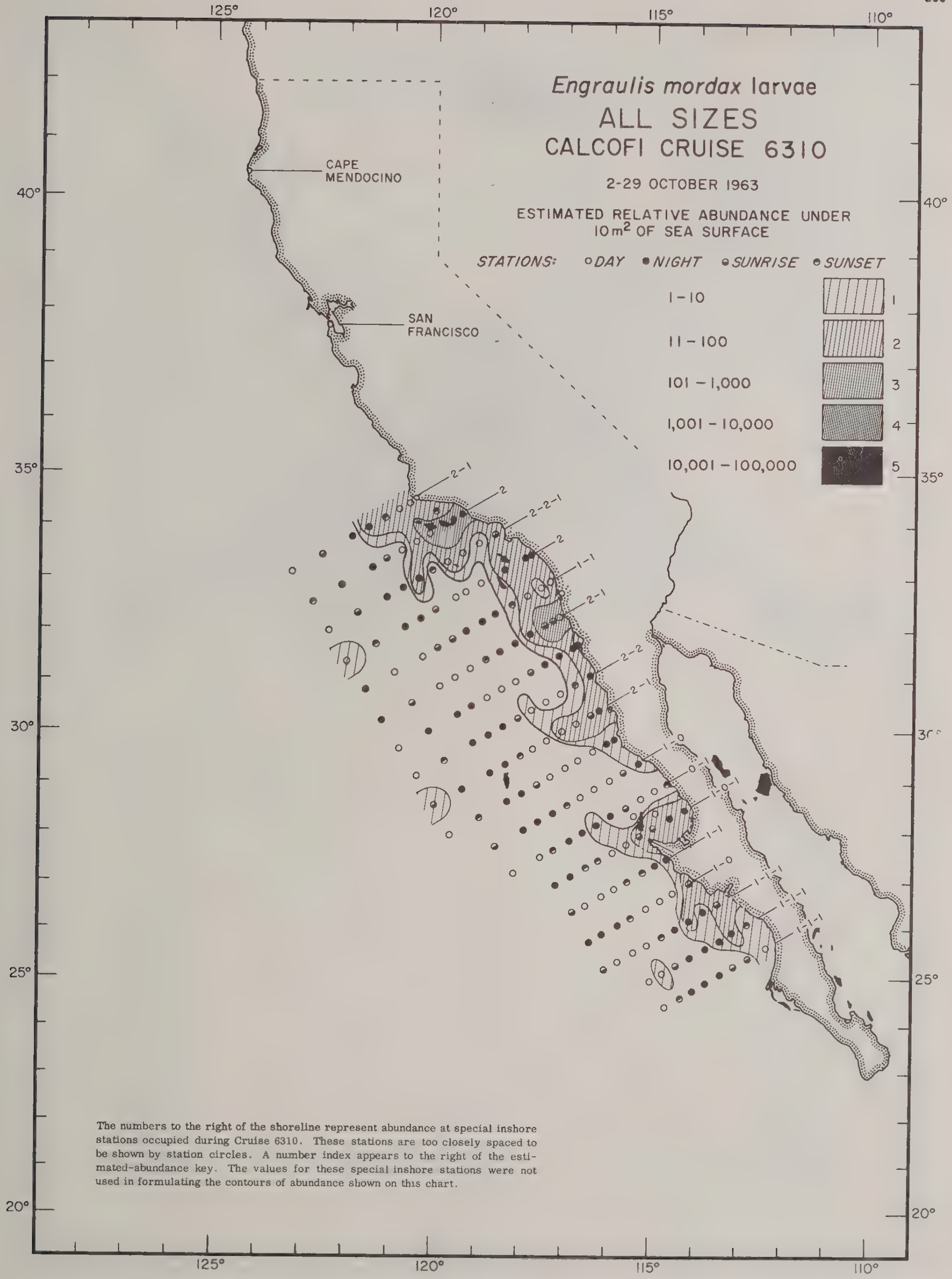

Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 6310
2-29 OCTOBER 1963
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◐SUNRISE ◑SUNSET
1-10 1
11-100 2
101-1,000 3
1,001-10,000 4
10,001-100,000 5
CAPE MENDOCINO
SAN FRANCISCO
125°
120°
115°
110°
40°
35°
30°
25°
20°
1-0
1
2-1-1
1
1-1
2-1
2-1
1-1
1-0
1-0-0
1-1
1-0
0-0-0
0-0-0
0-0-1

The numbers to the right of the shoreline represent abundance at special inshore stations occupied during Cruise 6310. These stations are too closely spaced to be shown by station circles. A number index appears to the right of the estimated-abundance key. The values for these special inshore stations were not used in formulating the contours of abundance shown on this chart.

Engraulis mordax larvae

Size Group: 6.26-12.25mm

6310

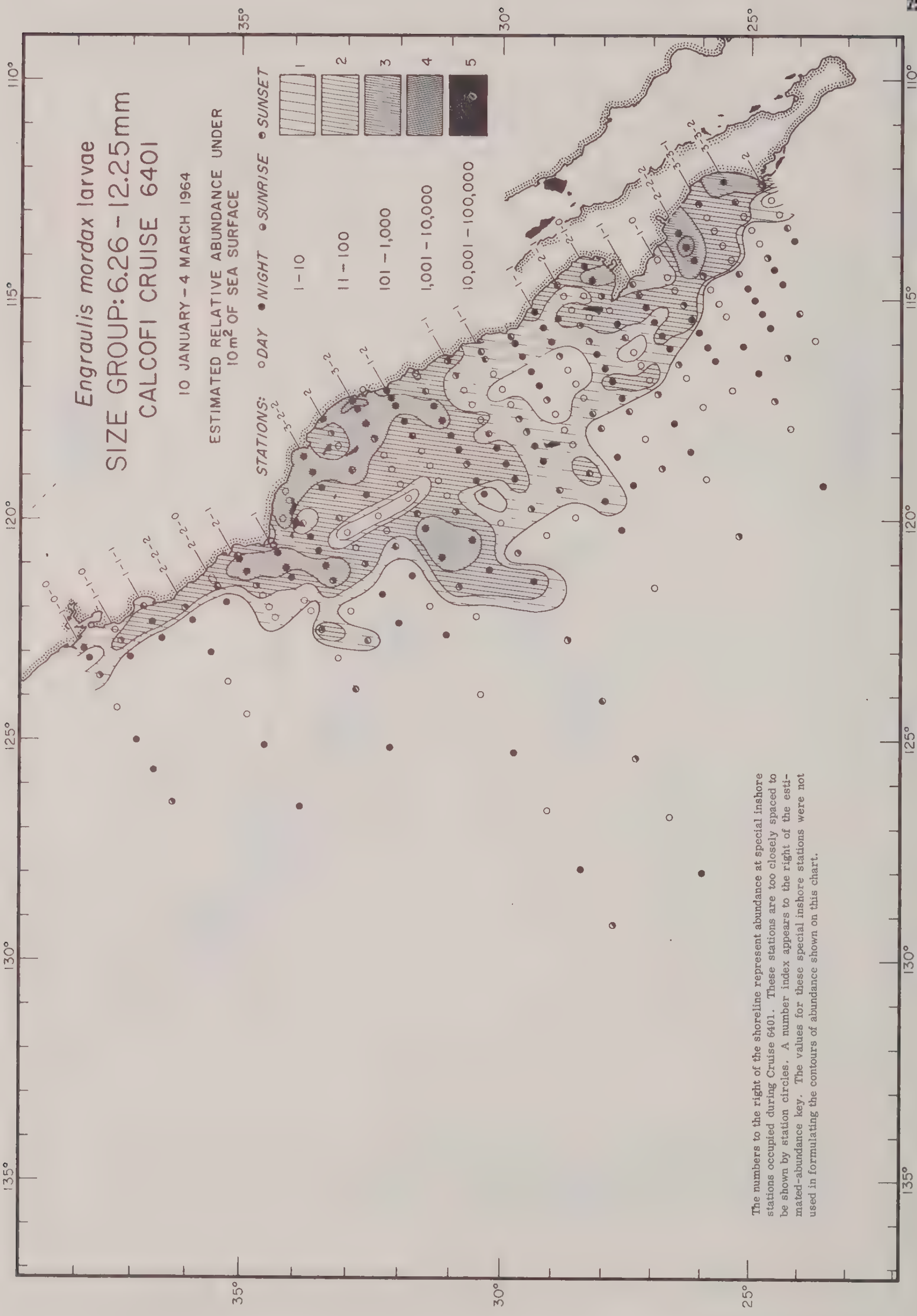

Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6310
2-29 OCTOBER 1963
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 – 10 ▨ 1
11 – 100 ▨ 2
101 – 1,000 ▨ 3
1,001 – 10,000 ▨ 4
10,001 – 100,000 ■ 5
CAPE MENDOCINO
SAN FRANCISCO
2-1
2
2-2-1
2
1-1
2-1
2-2
2-1
125°
120°
115°
110°
40°
35°
30°
25°
20°

The numbers to the right of the shoreline represent abundance at special inshore stations occupied during Cruise 6310. These stations are too closely spaced to be shown by station circles. A number index appears to the right of the estimated-abundance key. The values for these special inshore stations were not used in formulating the contours of abundance shown on this chart.

Engraulis mordax larvae

All Sizes

6310

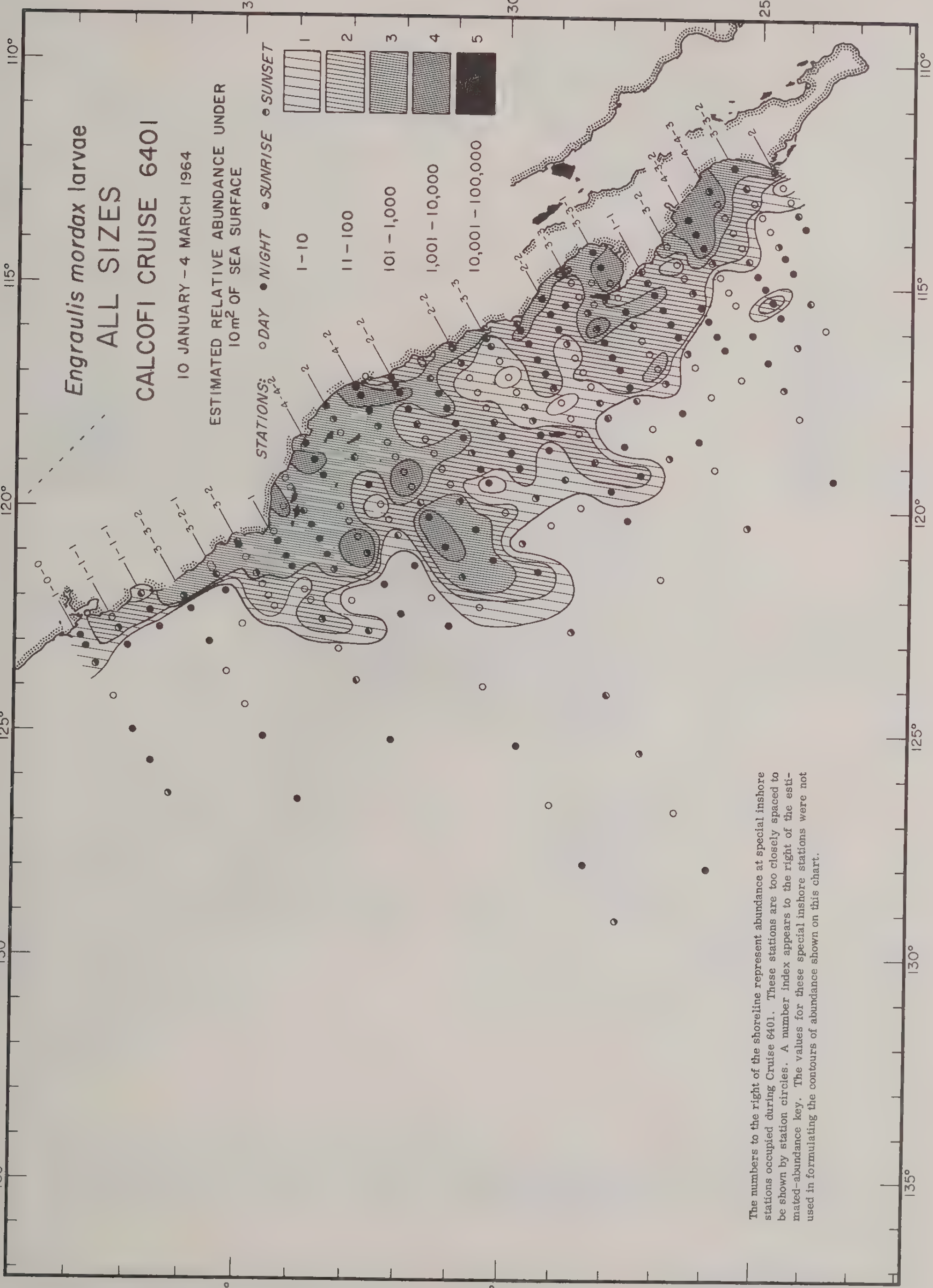

Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 6401
10 JANUARY - 4 MARCH 1964
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
1 - 10 — 1
11 - 100 — 2
101 - 1,000 — 3
1,001 - 10,000 — 4
10,001 - 100,000 — 5
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
110°
115°
120°
125°
130°
135°
35°
30°
25°

The numbers to the right of the shoreline represent abundance at special inshore stations occupied during Cruise 6401. These stations are too closely spaced to be shown by station circles. A number index appears to the right of the estimated-abundance key. The values for these special inshore stations were not used in formulating the contours of abundance shown on this chart.

Engraulis mordax larvae

Size Group: 6.26-12.25mm

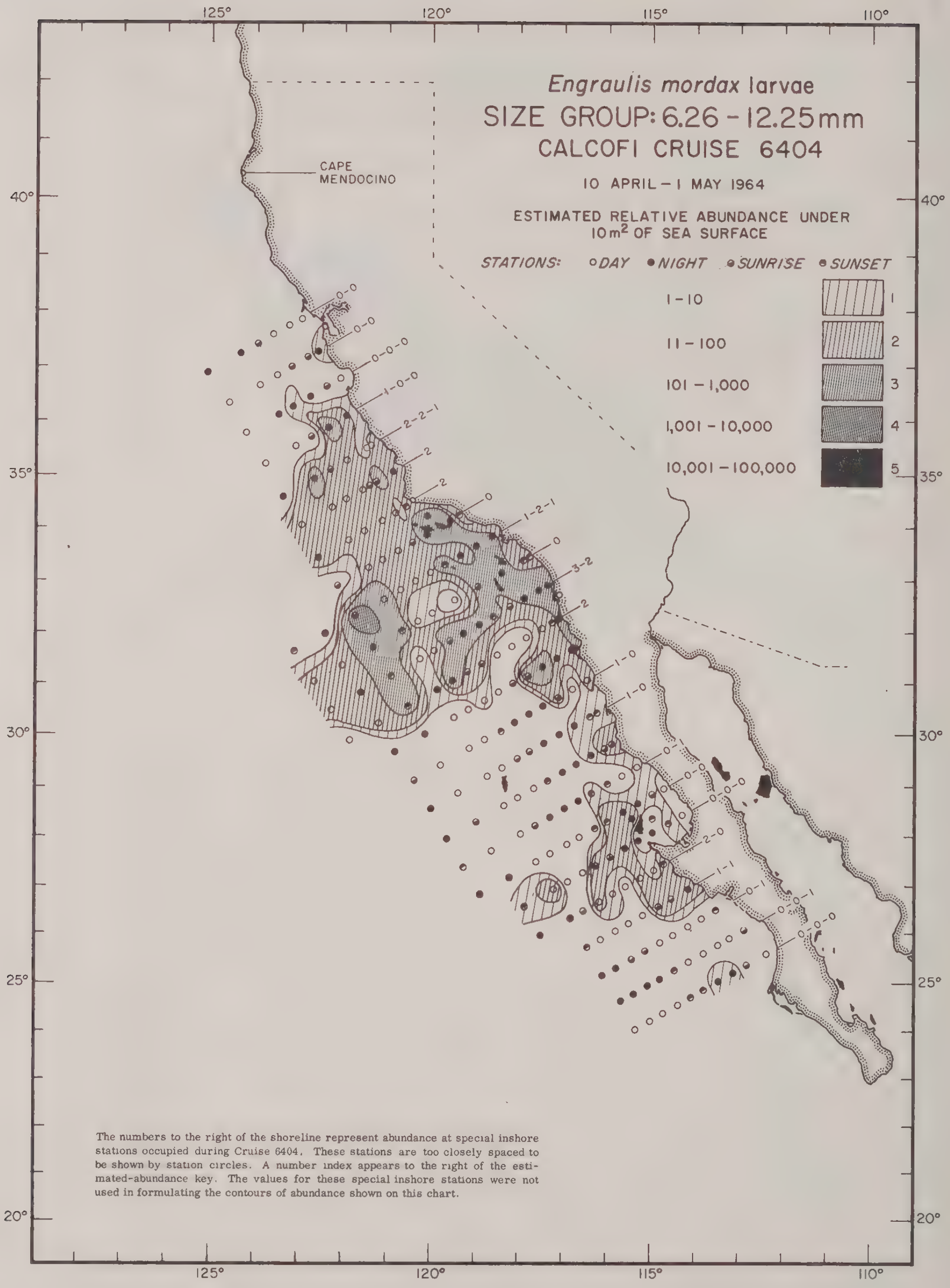
6401


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6401
10 JANUARY - 4 MARCH 1964
ESTIMATED RELATIVE ABUNDANCE UNDER
10 m² OF SEA SURFACE
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
1
2
3
4
5
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
110°
115°
120°
125°
130°
135°
35°
30°
25°
The numbers to the right of the shoreline represent abundance at special inshore stations occupied during Cruise 6401. These stations are too closely spaced to be shown by station circles. A number index appears to the right of the estimated-abundance key. The values for these special inshore stations were not used in formulating the contours of abundance shown on this chart.

Engraulis mordax larvae

All Sizes

6401

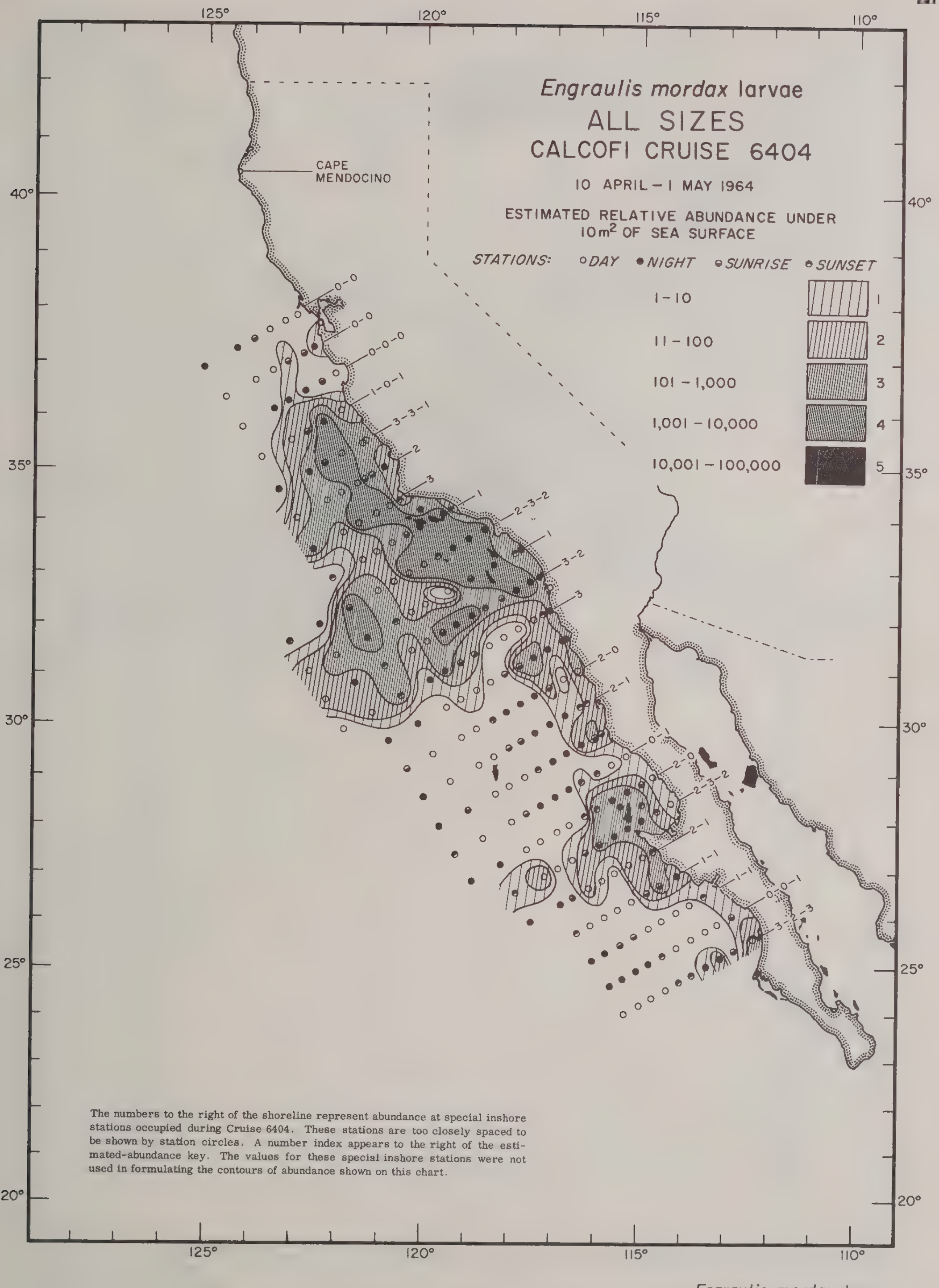

Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 6404
10 APRIL - 1 MAY 1964
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ●SUNRISE ●SUNSET
1-10 1
11-100 2
101-1,000 3
1,001-10,000 4
10,001-100,000 5
CAPE MENDOCINO
125°
120°
115°
110°
40°
35°
30°
25°
20°

The numbers to the right of the shoreline represent abundance at special inshore stations occupied during Cruise 6404. These stations are too closely spaced to be shown by station circles. A number index appears to the right of the estimated-abundance key. The values for these special inshore stations were not used in formulating the contours of abundance shown on this chart.

Engraulis mordax larvae

Size Group: 6.26-12.25mm

6404

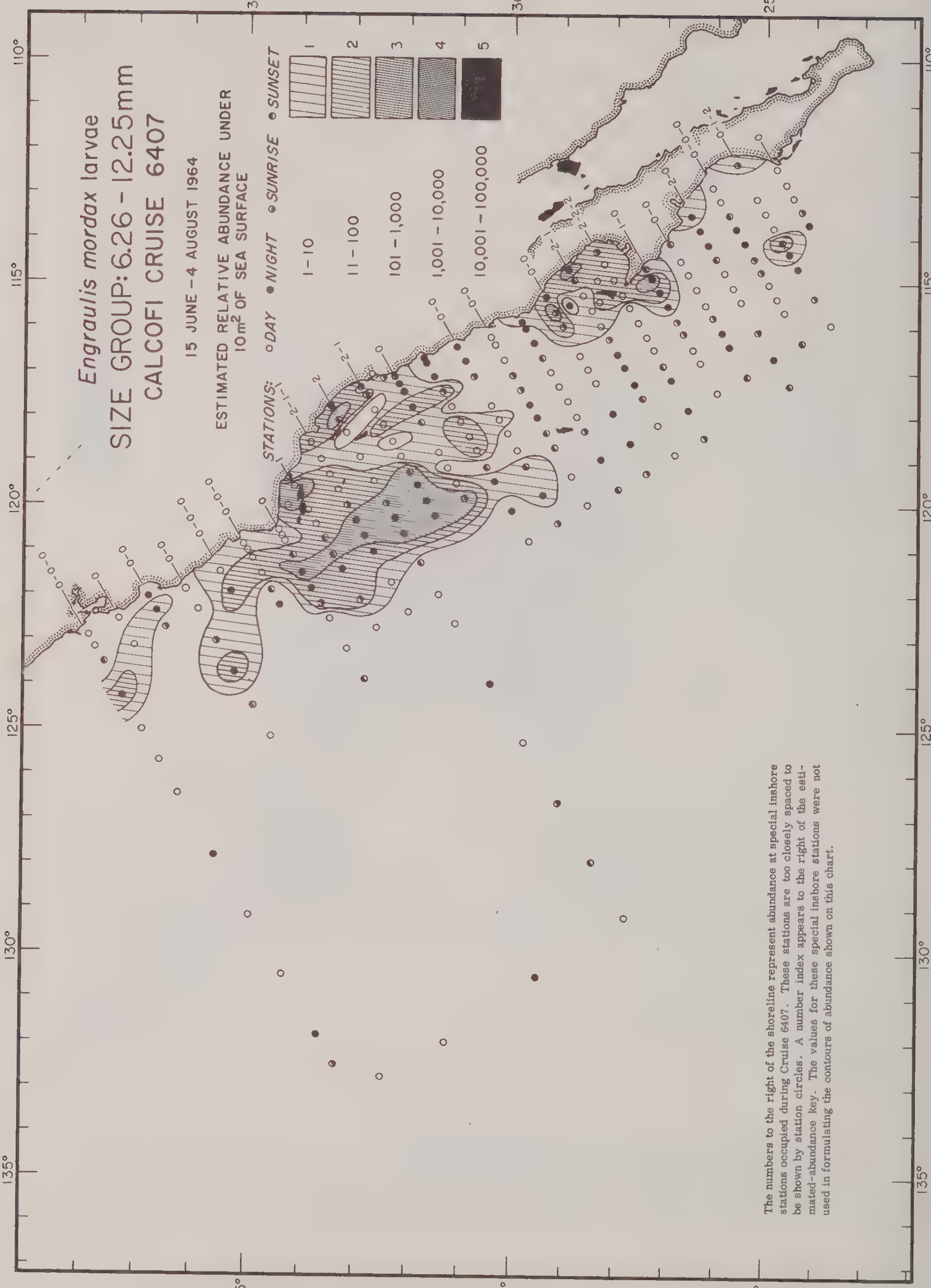

Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6404
10 APRIL – 1 MAY 1964
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ *DAY* ● *NIGHT* ◉ *SUNRISE* ◉ *SUNSET*
1 – 10 ▥ 1
11 – 100 ▥ 2
101 – 1,000 ▥ 3
1,001 – 10,000 ▩ 4
10,001 – 100,000 ■ 5
CAPE MENDOCINO
125°
120°
115°
110°
40°
35°
30°
25°
20°
0-0
0-0
0-0-0
1-0-1
3-3-1
2
3
1
2-3-2
1
3-2
3
2-0
2-1
0-1
2-0
2-3-2
2-1
1-1
1-1
0-1
3-2-3

The numbers to the right of the shoreline represent abundance at special inshore stations occupied during Cruise 6404. These stations are too closely spaced to be shown by station circles. A number index appears to the right of the estimated-abundance key. The values for these special inshore stations were not used in formulating the contours of abundance shown on this chart.

Engraulis mordax larvae

All Sizes

6404

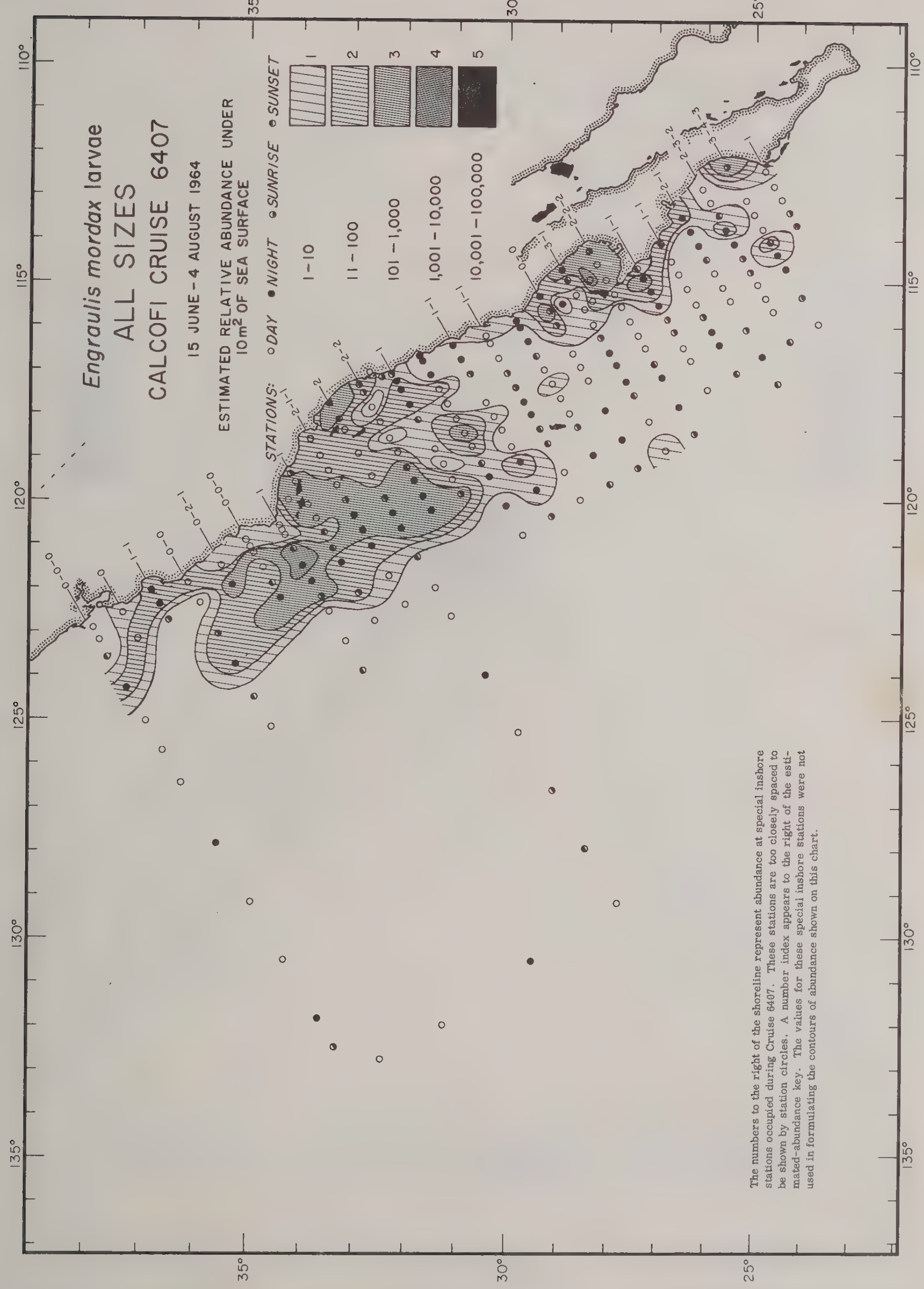

Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 6407
15 JUNE - 4 AUGUST 1964
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◐SUNRISE ◑SUNSET
1 1-10
2 11-100
3 101-1,000
4 1,001-10,000
5 10,001-100,000
110°
115°
120°
125°
130°
135°
35°
30°
25°

The numbers to the right of the shoreline represent abundance at special inshore stations occupied during Cruise 6407. These stations are too closely spaced to be shown by station circles. A number index appears to the right of the estimated-abundance key. The values for these special inshore stations were not used in formulating the contours of abundance shown on this chart.

Engraulis mordax larvae

Size Group: 6.26-12.25mm

6407

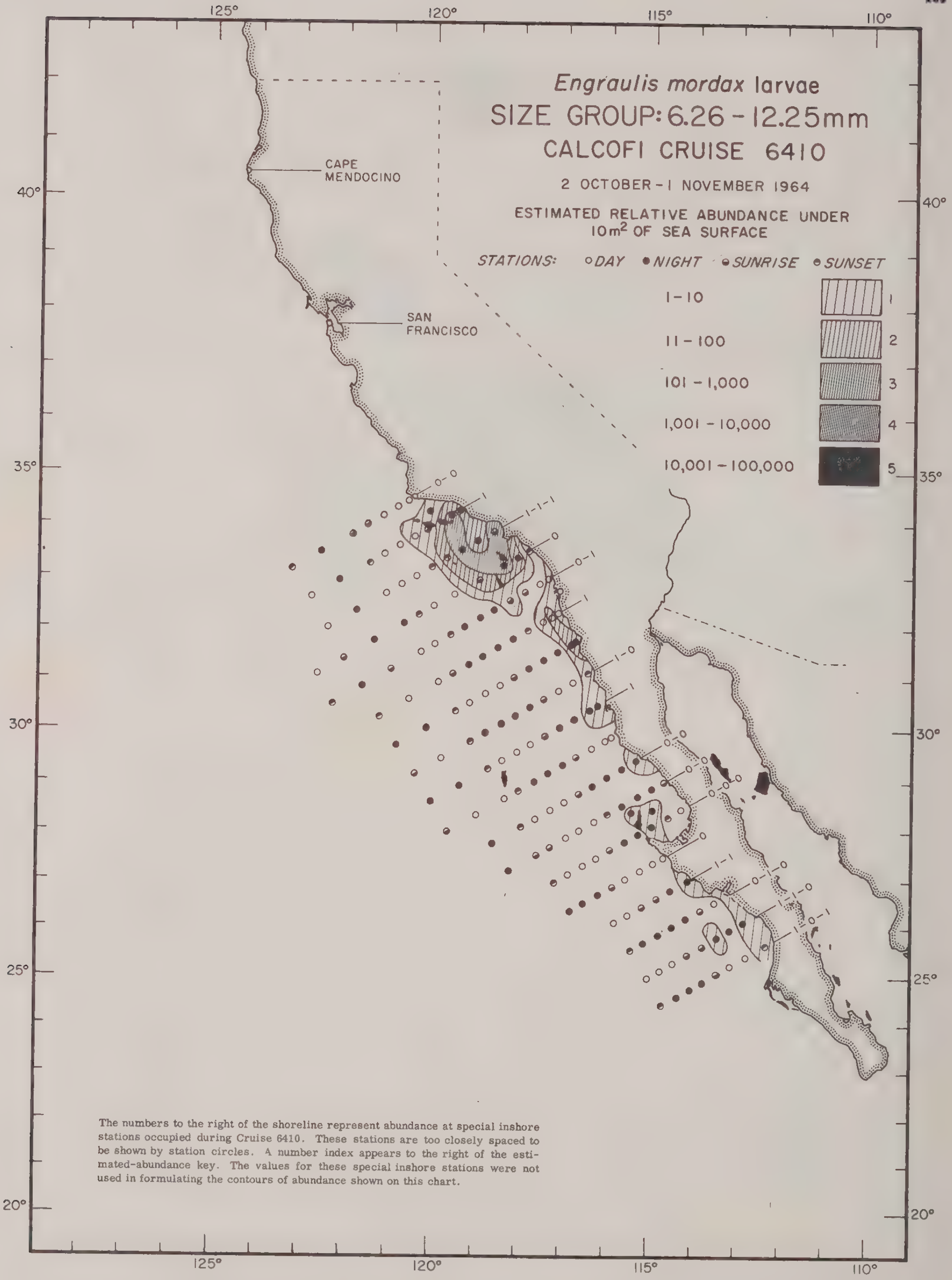

Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6407
15 JUNE - 4 AUGUST 1964
ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1-10 1
11-100 2
101-1,000 3
1,001-10,000 4
10,001-100,000 5
110°
115°
120°
125°
130°
135°
35°
30°
25°

The numbers to the right of the shoreline represent abundance at special inshore stations occupied during Cruise 6407. These stations are too closely spaced to be shown by station circles. A number index appears to the right of the estimated-abundance key. The values for these special inshore stations were not used in formulating the contours of abundance shown on this chart.

Engraulis mordax larvae

All Sizes

6407



Engraulis mordax larvae

SIZE GROUP: 6.26 - 12.25mm

CALCOFI CRUISE 6410

2 OCTOBER - 1 NOVEMBER 1964

ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE

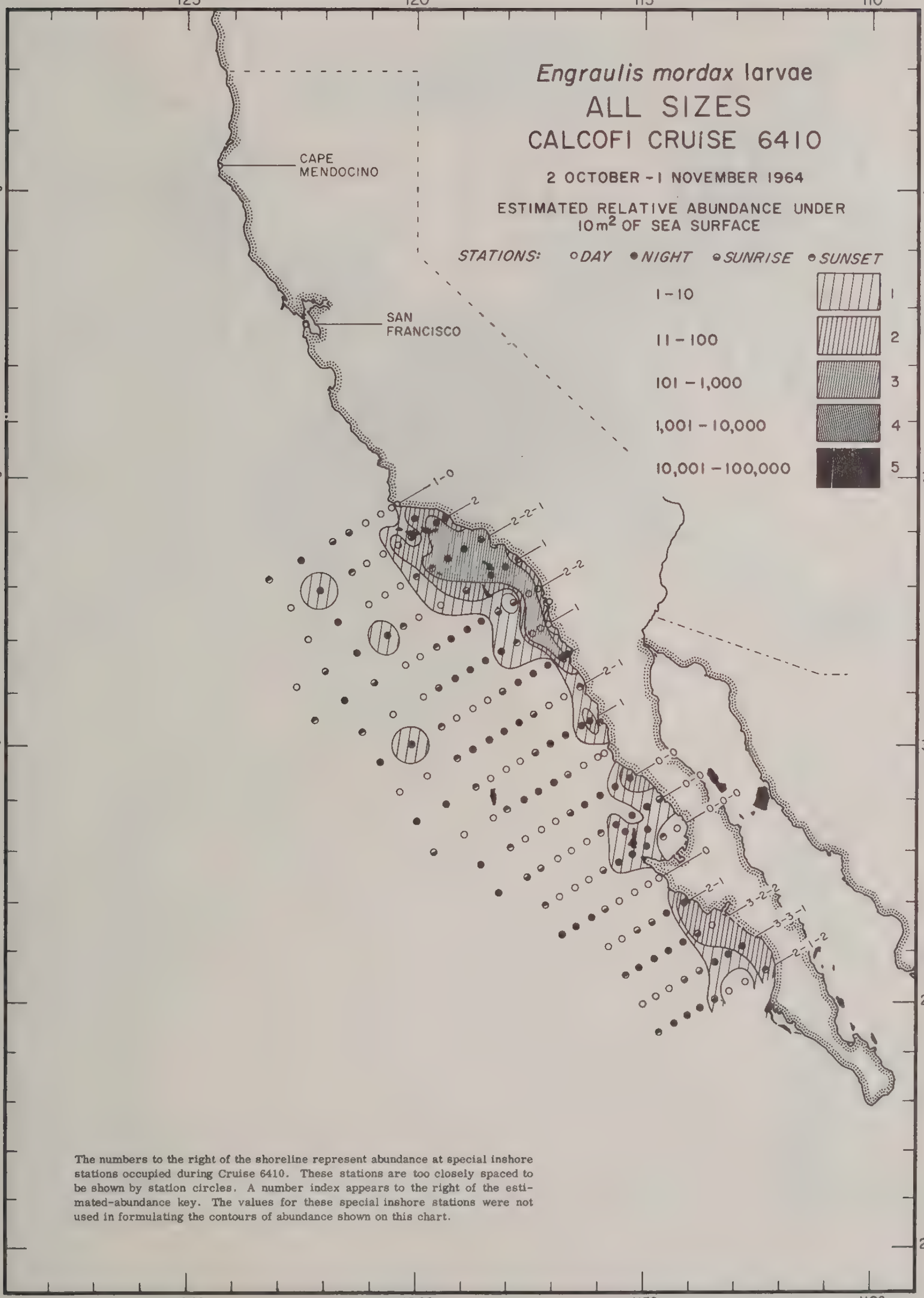
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1-10 1
11-100 2
101-1,000 3
1,001-10,000 4
10,001-100,000 5
CAPE MENDOCINO
SAN FRANCISCO
125°
120°
115°
110°
40°
35°
30°
25°
20°

The numbers to the right of the shoreline represent abundance at special inshore stations occupied during Cruise 6410. These stations are too closely spaced to be shown by station circles. A number index appears to the right of the estimated-abundance key. The values for these special inshore stations were not used in formulating the contours of abundance shown on this chart.

Engraulis mordax larvae

Size Group: 6.26-12.25mm

6410

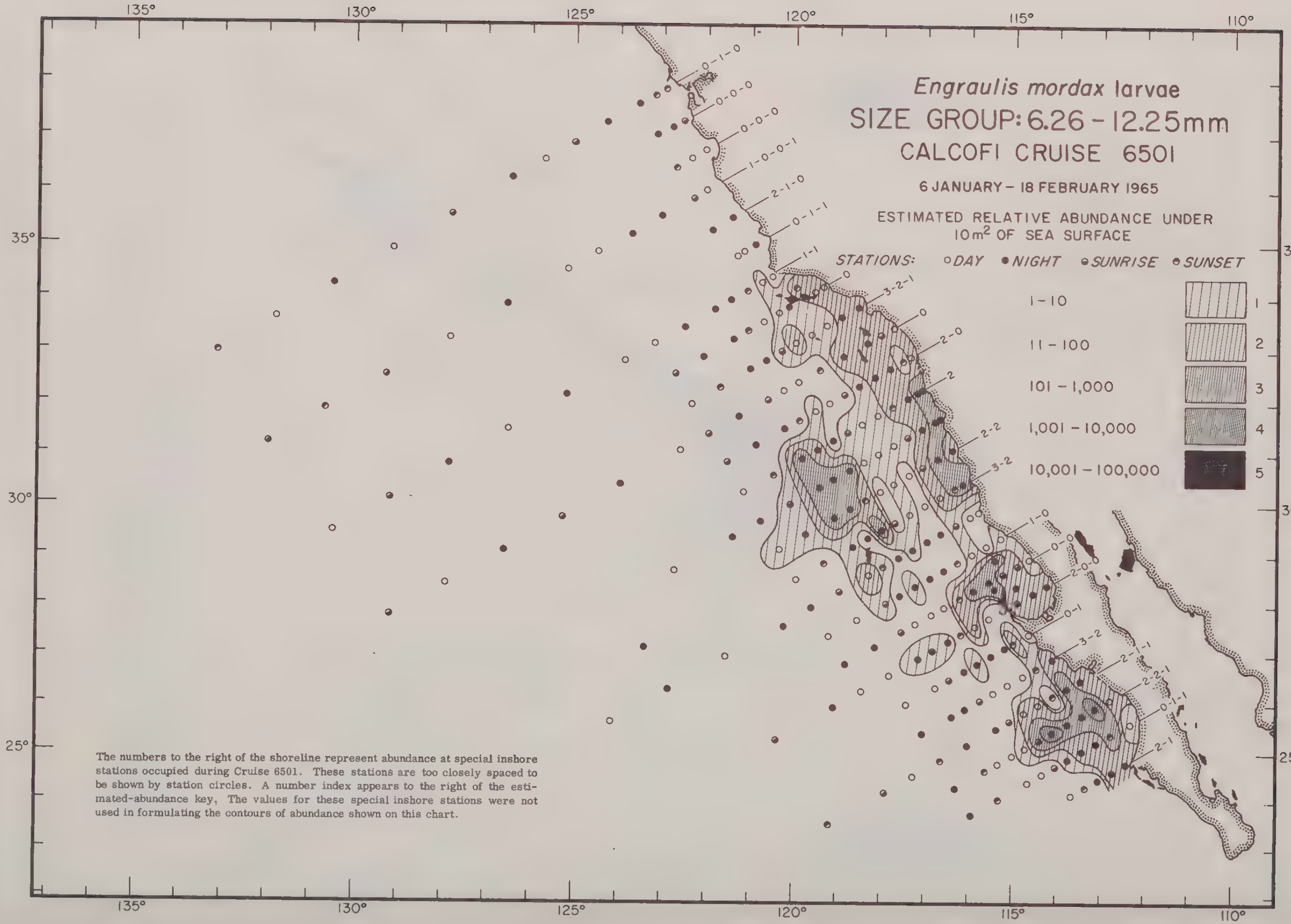

Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6410
2 OCTOBER - 1 NOVEMBER 1964
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1-10 1
11-100 2
101-1,000 3
1,001-10,000 4
10,001-100,000 5
CAPE MENDOCINO
SAN FRANCISCO
125°
120°
115°
110°
40°
35°
30°
25°
20°
1-0
2
2-2-1
1
2-2
1
2-1
1
0-0
0-0
0-0-0
0
2-1
3-2-2
3-3-1
2-1-2

The numbers to the right of the shoreline represent abundance at special inshore stations occupied during Cruise 6410. These stations are too closely spaced to be shown by station circles. A number index appears to the right of the estimated-abundance key. The values for these special inshore stations were not used in formulating the contours of abundance shown on this chart.

Engraulis mordax larvae

All Sizes

6410

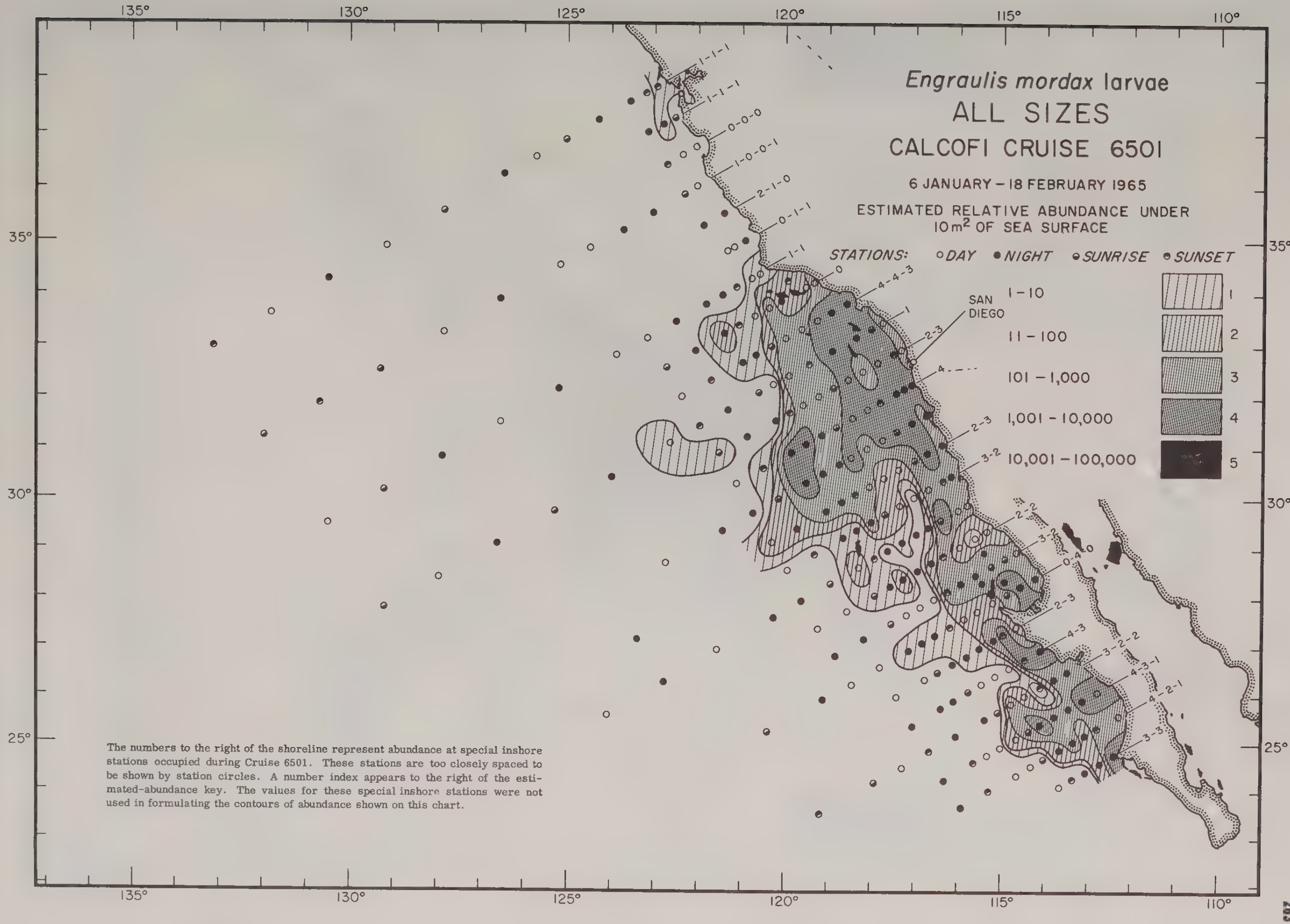

Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 6501
6 JANUARY - 18 FEBRUARY 1965
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◐SUNRISE ◑SUNSET
1-10 1
11-100 2
101-1,000 3
1,001-10,000 4
10,001-100,000 5
135°
130°
125°
120°
115°
110°
35°
30°
25°
0-1-0
0-0-0
0-0-0
1-0-0-1
2-1-0
0-1-1
1-1
3-2-1
0
2-0
2
2-2
3-2
1-0
0-0
2-0-0
0-1
3-2
2-1-1
2-2-1
0-1-1
2-1

The numbers to the right of the shoreline represent abundance at special inshore stations occupied during Cruise 6501. These stations are too closely spaced to be shown by station circles. A number index appears to the right of the estimated-abundance key. The values for these special inshore stations were not used in formulating the contours of abundance shown on this chart.

Engraulis mordax larvae

Size Group: 6.26-12.25mm

6501



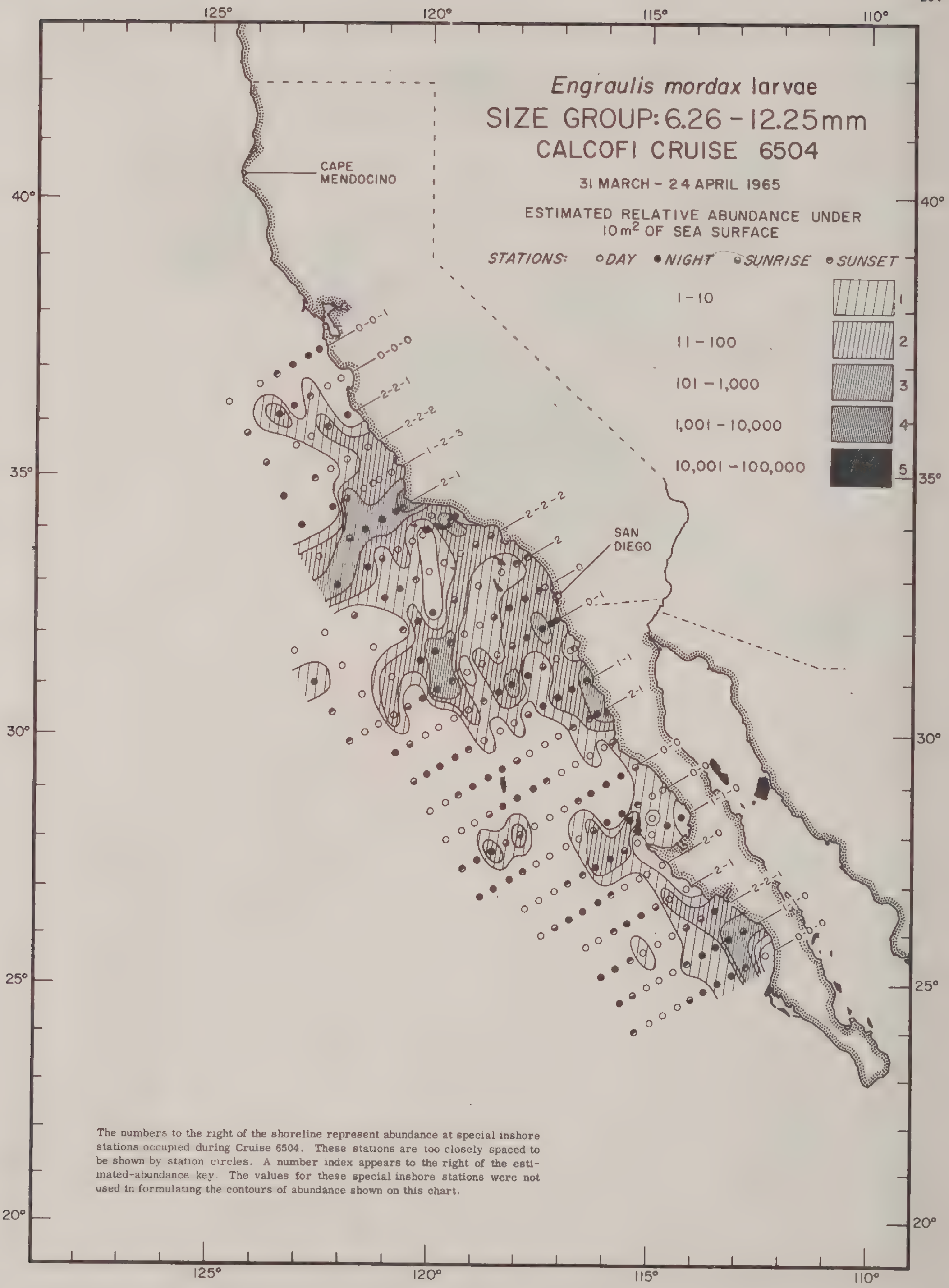
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6501

6 JANUARY – 18 FEBRUARY 1965

ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE

STATIONS: ○ DAY ● NIGHT ◐ SUNRISE ◑ SUNSET
1 – 10 ▨ 1
11 – 100 ▨ 2
101 – 1,000 ▨ 3
1,001 – 10,000 ▨ 4
10,001 – 100,000 ■ 5
SAN DIEGO
135°
130°
125°
120°
115°
110°
35°
30°
25°
1-1-1
1-1-1
0-0-0
1-0-0-1
2-1-0
0-1-1
1-1
0
4-4-3
1
2-3
4
2-3
3-2
2-2
3-2
0-4-0
2-3
4-3
3-2-2
4-3-1
4-2-1
3-3

The numbers to the right of the shoreline represent abundance at special inshore stations occupied during Cruise 6501. These stations are too closely spaced to be shown by station circles. A number index appears to the right of the estimated-abundance key. The values for these special inshore stations were not used in formulating the contours of abundance shown on this chart.

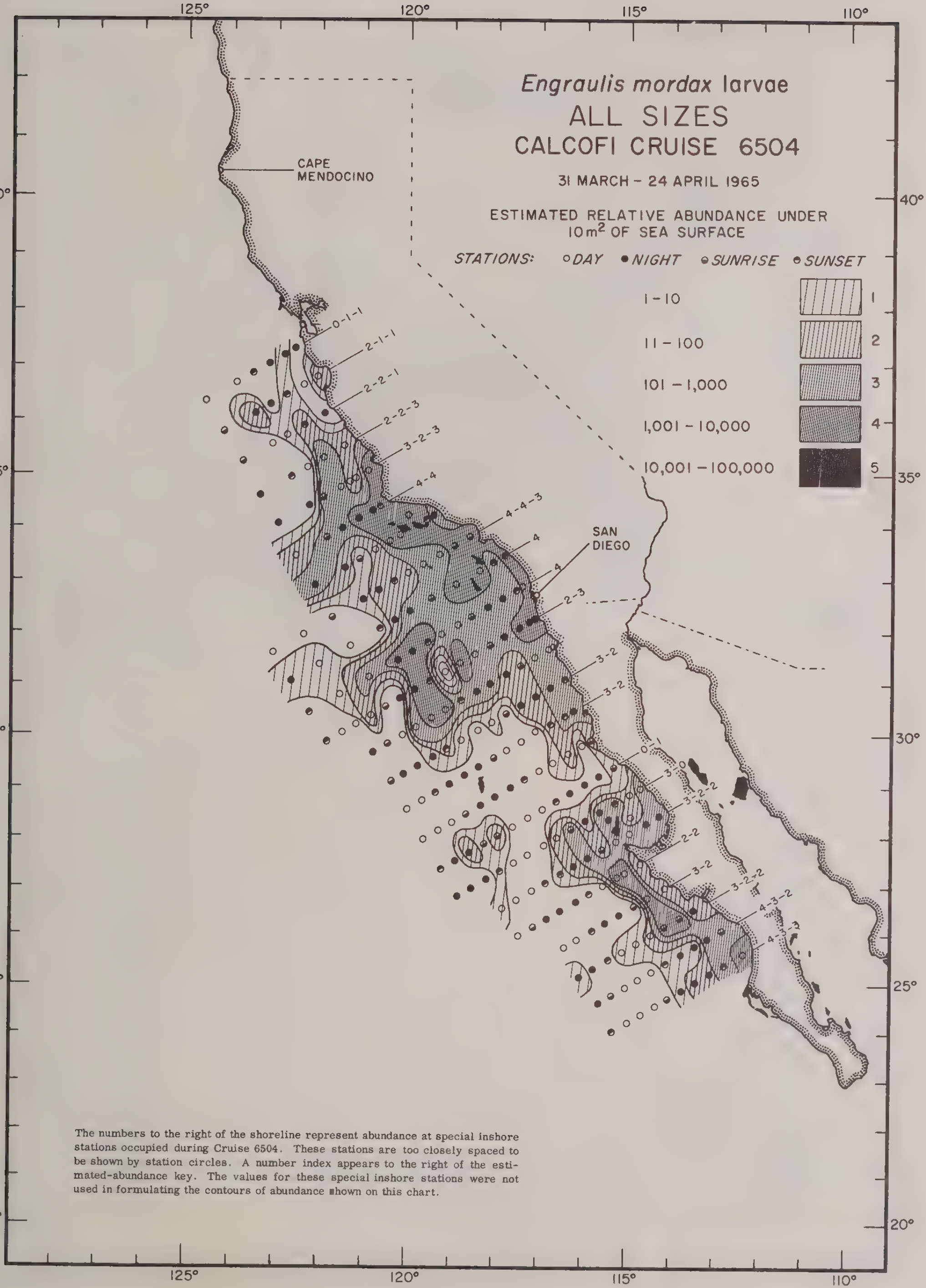

Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 6504
31 MARCH - 24 APRIL 1965
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT SUNRISE SUNSET
1 - 10 1
11 - 100 2
101 - 1,000 3
1,001 - 10,000 4
10,001 - 100,000 5
CAPE MENDOCINO
SAN DIEGO
0-0-1
0-0-0
2-2-1
2-2-2
1-2-3
2-1
2-2-2
2
0
0-1
1-1
2-1
0-0
0-0
1-1-0
2-0
2-1
2-2-1
1-1-0
0-0-0
125°
120°
115°
110°
40°
35°
30°
25°
20°

The numbers to the right of the shoreline represent abundance at special inshore stations occupied during Cruise 6504. These stations are too closely spaced to be shown by station circles. A number index appears to the right of the estimated-abundance key. The values for these special inshore stations were not used in formulating the contours of abundance shown on this chart.

Engraulis mordax larvae

Size Group: 6.26-12.25mm

6504



Engraulis mordax larvae

ALL SIZES

CALCOFI CRUISE 6504

31 MARCH – 24 APRIL 1965

ESTIMATED RELATIVE ABUNDANCE UNDER
10m² OF SEA SURFACE

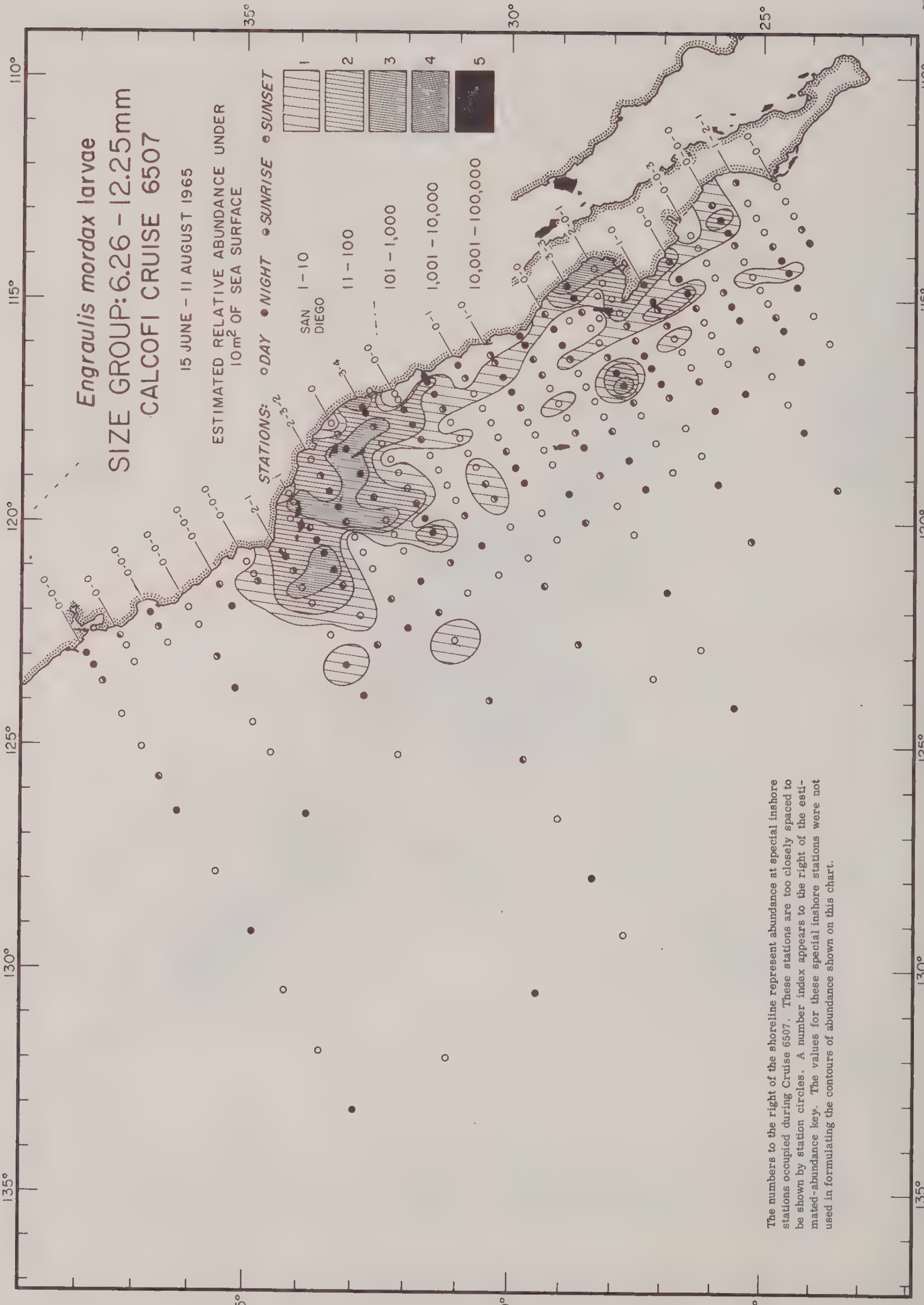
STATIONS: ○DAY ●NIGHT ◒SUNRISE ◓SUNSET
1 – 10 1
11 – 100 2
101 – 1,000 3
1,001 – 10,000 4
10,001 – 100,000 5
CAPE MENDOCINO
SAN DIEGO
125°
120°
115°
110°
40°
35°
30°
25°
20°
0-1-1
2-1-1
2-2-1
2-2-3
3-2-3
4-4
4-4-3
4
4
2-3
3-2
3-2
0-1
3-0
3-2-2
2-2
3-2
3-2-2
4-3-2
4-3-3

The numbers to the right of the shoreline represent abundance at special inshore stations occupied during Cruise 6504. These stations are too closely spaced to be shown by station circles. A number index appears to the right of the estimated-abundance key. The values for these special inshore stations were not used in formulating the contours of abundance shown on this chart.

Engraulis mordax larvae

All Sizes

6504

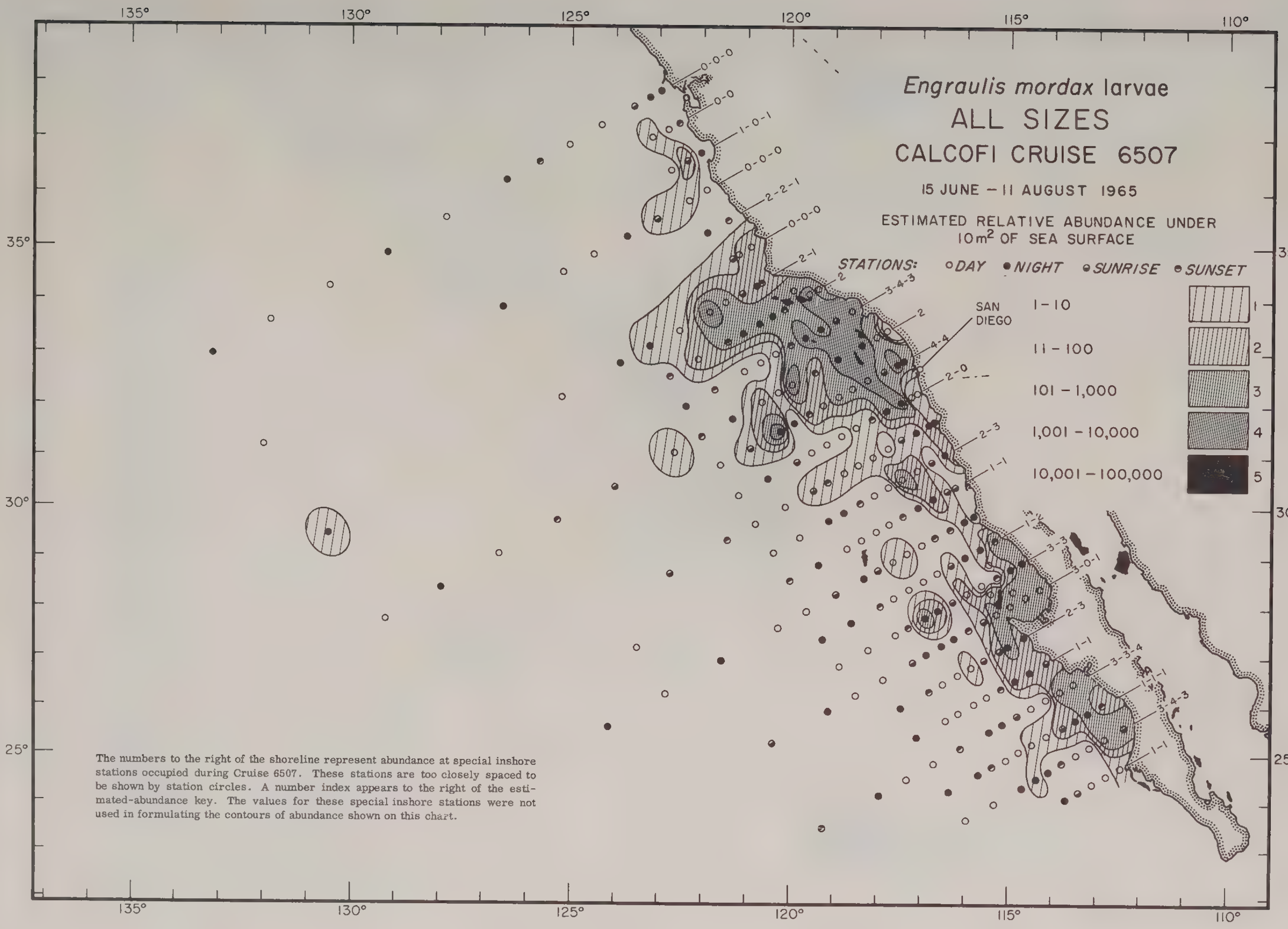

Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 6507
15 JUNE - 11 AUGUST 1965
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
1-10 — 1
11-100 — 2
101-1,000 — 3
1,001-10,000 — 4
10,001-100,000 — 5
STATIONS: ○DAY ●NIGHT ◐SUNRISE ◑SUNSET
SAN DIEGO
110°
115°
120°
125°
130°
135°
35°
30°
25°

The numbers to the right of the shoreline represent abundance at special inshore stations occupied during Cruise 6507. These stations are too closely spaced to be shown by station circles. A number index appears to the right of the estimated-abundance key. The values for these special inshore stations were not used in formulating the contours of abundance shown on this chart.

Engraulis mordax larvae

Size Group: 6.26-12.25mm

6507



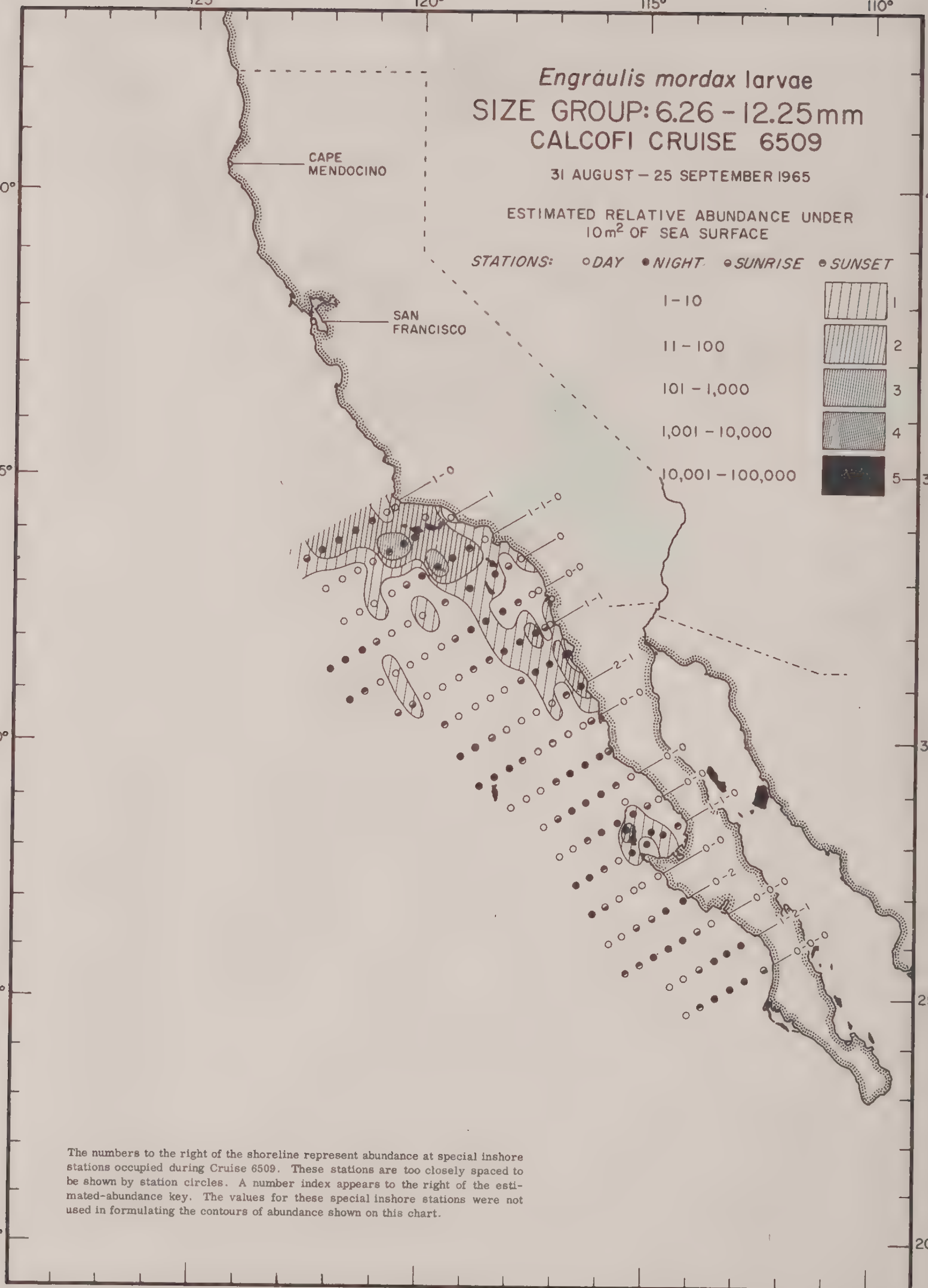
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6507
15 JUNE – 11 AUGUST 1965

ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE

STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1–10 ▤ 1
11–100 ▤ 2
101–1,000 ▤ 3
1,001–10,000 ▤ 4
10,001–100,000 ■ 5
SAN DIEGO
135°
130°
125°
120°
115°
110°
35°
30°
25°
0-0-0
0-0
1-0-1
0-0-0
2-2-1
0-0-0
2-1
2
3-4-3
2
4-4
2-0
2-3
1-1
1-2
3-3
3-0-1
2-3
1-1
3-3-4
1-1-1
3-4-3
1-1

The numbers to the right of the shoreline represent abundance at special inshore stations occupied during Cruise 6507. These stations are too closely spaced to be shown by station circles. A number index appears to the right of the estimated-abundance key. The values for these special inshore stations were not used in formulating the contours of abundance shown on this chart.

Engraulis mordax larvae
All Sizes
6507

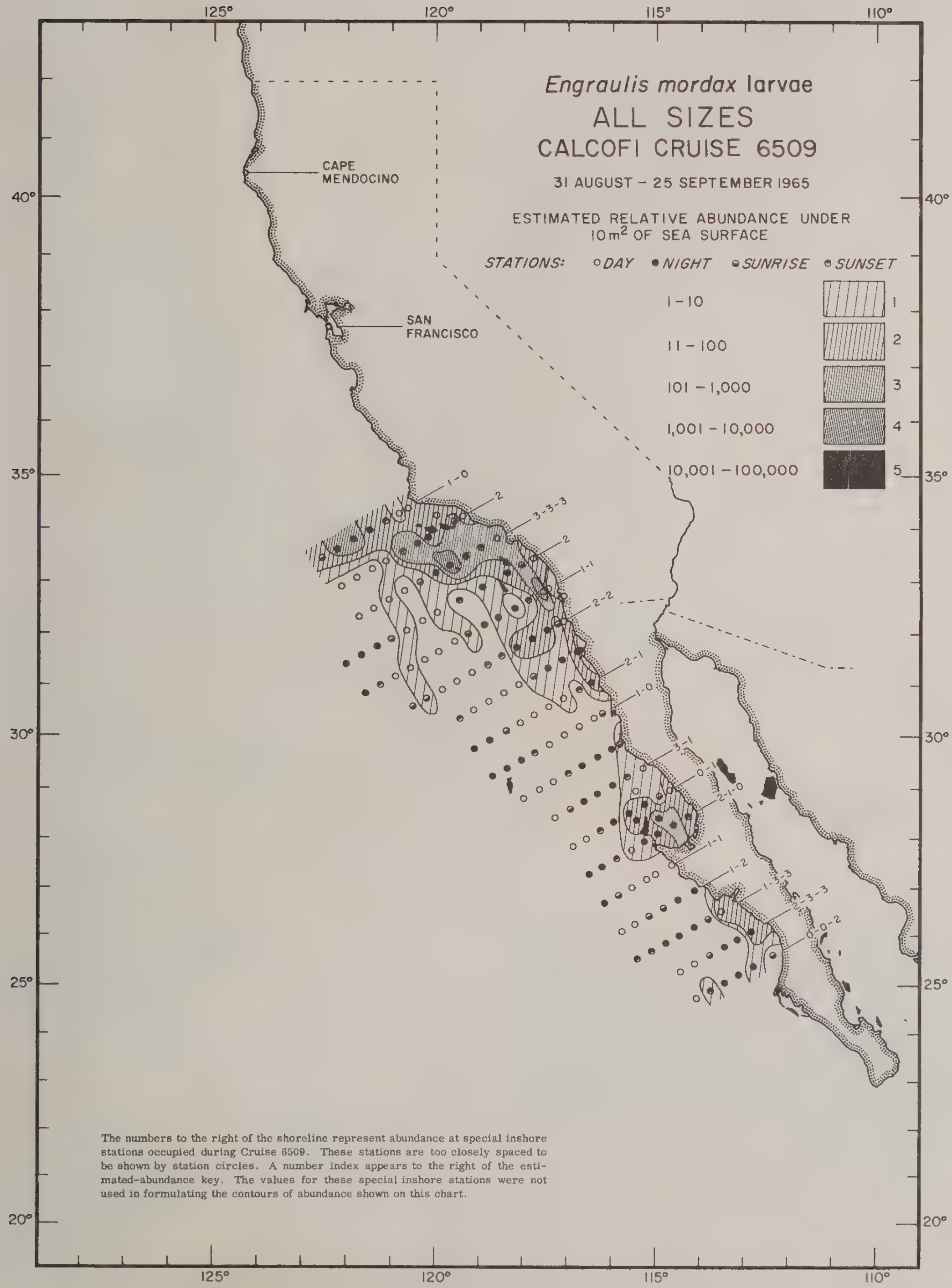

Engraulis mordax larvae
SIZE GROUP: 6.26 - 12.25mm
CALCOFI CRUISE 6509
31 AUGUST – 25 SEPTEMBER 1965
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 - 10 1
11 - 100 2
101 - 1,000 3
1,001 - 10,000 4
10,001 - 100,000 5
CAPE MENDOCINO
SAN FRANCISCO
125°
120°
115°
110°
40°
35°
30°
25°
20°
1-0
1
1-1-0
0
0-0
1-1
2-1
0-0
0-0
0-1-0
0-0
0-2
0-0-0
1-2-1
0-0-0

The numbers to the right of the shoreline represent abundance at special inshore stations occupied during Cruise 6509. These stations are too closely spaced to be shown by station circles. A number index appears to the right of the estimated-abundance key. The values for these special inshore stations were not used in formulating the contours of abundance shown on this chart.

Engraulis mordax larvae

Size Group: 6.26-12.25mm

6509

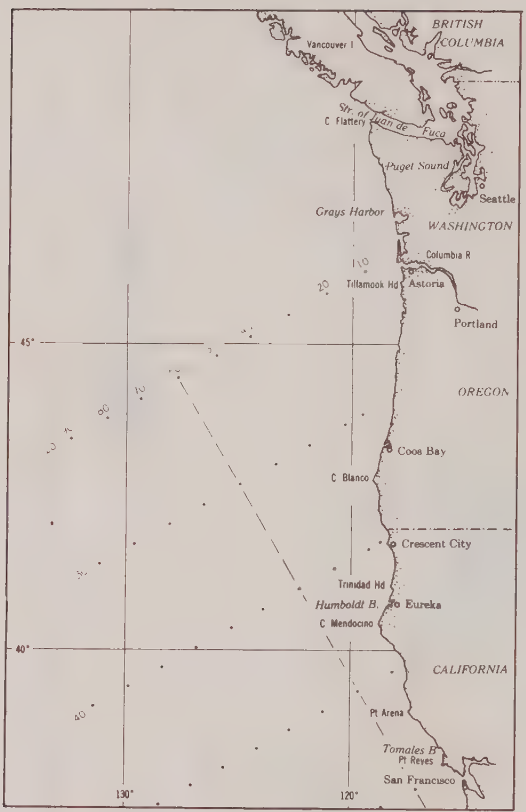

125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6509
31 AUGUST – 25 SEPTEMBER 1965
ESTIMATED RELATIVE ABUNDANCE UNDER 10 m² OF SEA SURFACE
STATIONS: ○ DAY ● NIGHT ◒ SUNRISE ◓ SUNSET
1 – 10 1
11 – 100 2
101 – 1,000 3
1,001 – 10,000 4
10,001 – 100,000 5
CAPE MENDOCINO
SAN FRANCISCO
1-0
2
3-3-3
2
1-1
2-2
2-1
1-0
3-1
0-1
2-1-0
1-1
1-2
1-3-3
2-3-3
0-0-2

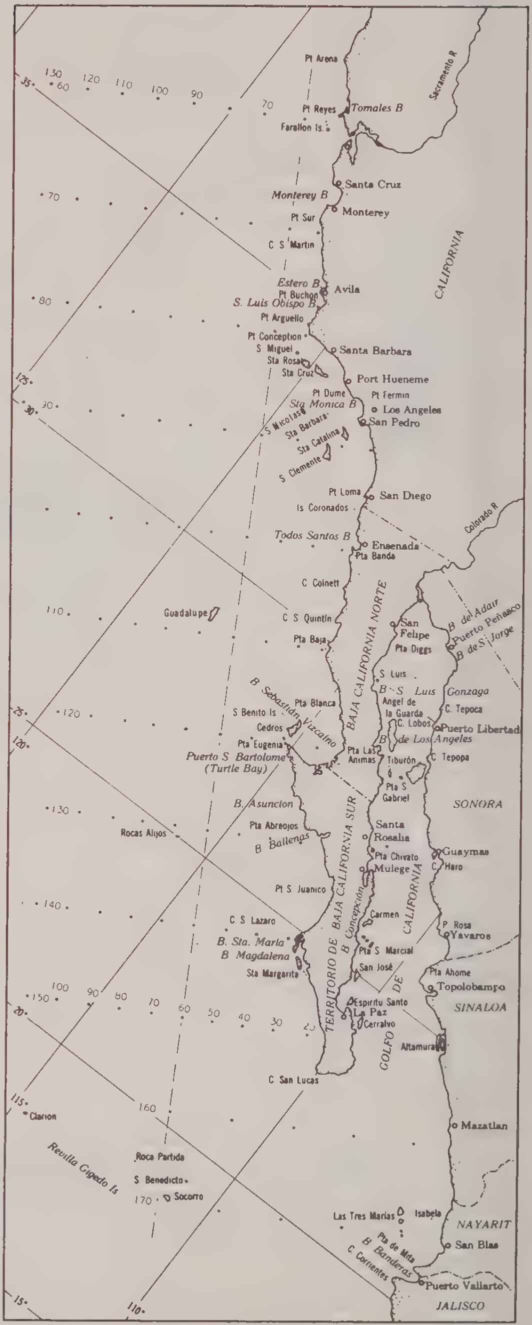
The numbers to the right of the shoreline represent abundance at special inshore stations occupied during Cruise 6509. These stations are too closely spaced to be shown by station circles. A number index appears to the right of the estimated-abundance key. The values for these special inshore stations were not used in formulating the contours of abundance shown on this chart.

Engraulis mordax larvae

All Sizes

6509


BRITISH COLUMBIA
Vancouver I
Str. of Juan de Fuca
C Flattery
Puget Sound
Seattle
Grays Harbor
WASHINGTON
Columbia R
110
20
Tillamook Hd
Astoria
Portland
45°
OREGON
10
Coos Bay
C Blanco
Crescent City
Trinidad Hd
Humboldt B.
Eureka
C Mendocino
40°
CALIFORNIA
40
Pt Arena
Tomales B
Pt Reyes
San Francisco
130°
120°


Pt Arena
Sacramento R
130
120
110
100
90
35°
60
70
Pt Reyes
Tomales B
Farallon Is.
Santa Cruz
Monterey B
Monterey
Pt Sur
C S Martin
CALIFORNIA
Estero B
Pt Buchon
Avila
S. Luis Obispo B.
80
Pt Arguello
Pt Conception
S Miguel
Santa Barbara
Sta Rosa
Sta Cruz
Port Hueneme
125°
Pt Dume
Pt Fermin
Sta Monica B
Los Angeles
30°
S Nicolas
Sta Barbara
San Pedro
Sta Catalina
S Clemente
Pt Loma
San Diego
Is Coronados
Colorado R
Todos Santos B
Ensenada
Pta Banda
C Colnett
BAJA CALIFORNIA NORTE
B de Adair
Puerto Peñasco
B de S Jorge
110
Guadalupe
C S Quintin
San Felipe
Pta Diggs
Pta Baja
S Luis
B S Luis Gonzaga
Angel de la Guarda
C. Tepoca
B Sebastian Vizcaino
Pta Blanca
S Benito Is
25°
120
Cedros
C. Lobos
Puerto Libertad
B de Los Angeles
120°
Pta Eugenia
Pta Las Animas
Tiburon
C Tepopa
Puerto S Bartolome (Turtle Bay)
Pta S Gabriel
B. Asuncion
SONORA
130
Rocas Alijos
Pta Abreojos
Santa Rosalia
B Ballenas
Pta Chivato
Guaymas
Mulege
C. Haro
Pt S Juanico
TERRITORIO DE BAJA CALIFORNIA SUR
B Concepcion
140
Carmen
C S Lazaro
GOLFO DE CALIFORNIA
P. Rosa
Yavaros
B. Sta. Maria
B Magdalena
Pta S Marcial
Sta Margarita
San José
Pta Ahome
100
90
80
70
60
50
40
30
150
Topolobampo
Espiritu Santo
La Paz
SINALOA
20°
Cerralvo
Altamura
C San Lucas
115°
160
Clarion
Mazatlan
Revilla Gigedo Is
Roca Partida
S Benedicto
170
Socorro
Las Tres Marias
Isabela
NAYARIT
Pta de Mita
B Banderas
San Blas
C Corrientes
Puerto Vallarto
15°
110°
JALISCO

These maps are designed to show essential details of the area most intensively studied by the California Cooperative Oceanic Fisheries Investigations. This is approximately the same area as is shown in color on the front cover. Geographical place names are those most commonly used in the various publications emerging from the research. The cardinal station lines extending southwestward from the coast are shown. They are 120 miles apart. Additional lines are utilized as needed and can be as closely spaced as 12 miles apart and still have individual numbers. The stations along the lines are numbered with respect to the station 60 line, the numbers increasing to the west and decreasing to the east. Most of them are 40 miles apart, and are numbered in groups of 10. This permits adding stations as close as 4 miles apart as needed. An example of the usual identification is 120.65. This station is on line 120, 20 nautical miles southwest of station 60.

The projection of the front cover is Lambert's Azimuthal Equal Area Projection. The detail maps are a Mercator projection.

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